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Adverse Conditions as Inhibitors of Ecdysis in the Lobster *Homarus americanus*[1]

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ABSTRACT

The molting incidence for male lobsters (*Homarus americanus*) subjected to a variety of conditions was compared with that for free male lobsters. The data show that, for free western Newfoundland lobsters, molting reached the 90% level by the end of September. During the same period, mildly restrictive conditions reduced the molting incidence to 50% or less, and when lobsters held under these conditions were also tagged or marked the molting incidence was reduced to 30% or less. A reduction in molting, equivalent to or greater than that produced by tagging or marking plus mildly restrictive conditions, was achieved by highly restrictive conditions which enforced a high degree of association between lobsters. The diets used in these experiments did not appear to have any influence on the molting incidence. The data suggested that darkness plus starvation under highly restrictive conditions was even more inhibitory than any of the other conditions applied. Other light intensities tested under the highly restrictive conditions had no apparent effect on the molting incidence; however, stimulation of molting by light could have been negated by the inhibitory effects of this form of captivity.

INTRODUCTION

It was established early in studies on the lobster (*Homarus americanus* Milne-Edwards) that ecdysis occurs every year for adult males and every second year for adult females (Herrick, 1911). Templeman (1939) and Wilder (1953) have shown that this is also essentially true for lobsters in colder, northern waters. The lowest molting incidences for lobsters recorded by Wilder (1953) for the 1948–49 season were for the Port Maitland (89% of the males, 77% of the females) and L'Archeveque (89% of the males) areas of Nova Scotia. Herrick (1911) suggested that the intermolt period could be prolonged by "any influence which retards growth or unduly taxes the vital energies" of the lobsters. Emmel's (1906) study of juvenile lobsters, in which he showed the molt inhibiting effect of the injury-provoked regenerative process, would tend to bear this out. Studies have been made, however, which show that injury may actually initiate the molting process in some of the other species (Passano, 1960b).

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Work to establish the best conditions of captivity, to determine indices of dietary adequacy (Stewart et al., 1967b), to assess tagging and marking methods and to acquire information on the growth rate of lobsters in nature illustrates the relative importance of adverse conditions as inhibitors of lobster ecdysis.

EXPERIMENTAL

The locations of the different areas in which lobsters were obtained or held captive is shown in Fig. 1.

FIG. 1. Locations (arrows) from which the lobsters were obtained or where they were held captive.

LOBSTER TAGS

(*a*) The "dart tag" used was a modified form of the Floy[2] Tag No. 6: a simple nylon arrow with an attached yellow vinyl tube pushed close to the arrowhead. This tag was inserted into the abdominal muscle, left or right of the mid line, between the 2nd and 3rd segments dorsally or in the 2nd segment ventrally.

(*b*) The "ferromagnetic tag" was a 1-mm long piece of wire (0.25 mm diam) marked with one narrow stripe of colored polyvinyl chloride. Ten colors were used, each representing a different lobster length category. A tag was inserted into a hypodermic needle and ejected from the needle with a wire plunger after the needle was inserted into the basis muscle of the 2nd left

[2]Floy Tag Manufacturing Co., Seattle, Wash.

pleopod or left uropod of the lobster. Its presence was detected by a magnetometer modified for the purpose and built by Dr K. B. Jefferts[3].

Western Newfoundland Lobsters — Free and Mildly Restrictive Conditions

Free lobsters.— Samples of male lobsters were taken at random from indiscriminate trappings of local populations. The lobsters were divided into two categories, molted that year or not molted that year, on the basis of an external examination of their shells (the reliability of this data was improved by having one experienced person only making the examinations). The old shell (not molted this year) in contrast with a new shell (molted this year) tends to be faded in color, has more epifaunal growth, and is harder and rougher. The examinations were made over a considerable time range (months) thus avoiding the distortion in molting percentages which could result from data collected immediately before and after molting. These differences would stem from data for the low "catchability" period of the lobster in the immediate pre-ecdysal state being compared with data for the high "catchability" period of the lobster in the immediate post-ecdysal state.

Marked and released.— Lobsters held in lobster "crates" under crowded conditions for 3–21 days were marked with a dart tag or with holes bored in the tail fan as described by Wilder (1953) and were released in the area of capture.

Mildly restrictive conditions.— Lobsters held not more than 2 days were transferred to wire mesh cages where they were held captive singly. The cages (90 × 90 × 25 cm high) were kept at a depth of 5 m on the lobster grounds and their occupants were fed a diet of scallop gonads and mantles (approximately 500 g/animal per week) by a Scuba[4] diver.

Some of these lobsters were marked (dart tags, holes in the tail fan, or ferromagnetic tags) and others were unmarked. All of the lobsters were measured before and after the molting period (late September to early October) to determine whether molting had occurred.

Fourchu, Nova Scotia Lobsters — Highly Restrictive Conditions

Approximately 500 healthy, hard-shelled, male lobsters (average weight 580 g), captured at Fourchu, Nova Scotia (20 miles north of L'Archeveque) in the first half of July 1964, were transferred to our laboratory and held in a continuous-flow seawater aquarium (water flow, 10 liters/min equalled two complete changes per hour of sea water; ambient external seawater temperatures; salt content, 3.3%) (Stewart and Power, 1963). Both large chelae were closed with rubber bands immediately upon capture. The most vigorous and uninjured animals were distributed in groups of 25 to each of 15 (90 × 90 cm) tanks in which the seawater level was maintained at a depth of 35 cm. Each tank was supplied with a compartmented shelter.

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[3]74 Possum Way, Murray Hill, N.J.
[4]Self-contained underwater breathing apparatus.

An excess of food was placed on the floor of seven of the tanks and the uneaten food was removed just prior to the next feeding. The animals were fed on Mondays, Wednesdays, and Fridays. The diet was beef liver and herring, given separately on alternate feeding days. The remaining eight tanks of lobsters were not supplied with food.

Tanks of fed and starved lobsters were exposed to different light intensities for a total daily period of 14 hr as described previously (Stewart et al., 1967b). Four levels of light were employed: 0, 8, 24, and 40 lumens per sq ft. Thus about 50 fed and 50 starved lobsters were exposed to each of the 4 different light levels except at 8 lumens per foot^2 where 25 fed and 50 starved animals were exposed. At the end of the experiment, serum protein, hemocyte, and muscle values were determined for approximately half the lobsters (reported previously in Stewart et al., 1967b, and identified there as groups 9–16).

Shelters

Our shelters, made of 3-mm black lucite, were 90 × 37 cm and contained 24 compartments. The compartments were arranged in two tiers with upper compartments at right angles to those in the bottom tier (eight openings on each side of the lower tier and four at each end of the upper tier). All surfaces of the shelter were pierced with numerous 6-mm diam holes to permit the free flow of sea water. The individual compartments were approximately 18.5 × 10 × 7.5 cm high. The weighted compartment itself was placed in the center of the tank leaving approximately 26 cm of free space on two sides.

The lobsters, after an initial period lasting from a few minutes to several hours, ceased explorations and occupied the shelters on a more or less permanent basis. There were always one, two, or three lobsters, however, which did not remain in the shelters but roamed around the tank.

Molting

The tanks were checked at hourly intervals and the time of ecdysis was recorded. The lobster casting its shell was removed from the tank as soon as it partially or completely emerged from the old shell. On a few occasions when ecdysis occurred between observations the soft lobster was attacked and partially eaten. This cannibalism was rare due to the close watch kept on the tanks, but it seemed to occur as readily among the fed as it did among the starved lobsters.

RESULTS AND DISCUSSION

The data in Table I show that in western Newfoundland molting of free lobsters reached or exceeded the 90% level by the end of September shortly after the period of highest water temperatures. The data also demonstrate that the natural molting incidence in this area is comparable with that reported by Wilder (1953) for Nova Scotia lobsters. This is in marked contrast to the incidence recorded for lobsters captured and held in these same areas

TABLE I. Temperatures on the lobster grounds and natural molting incidence of male lobsters observed in random samples from western Newfoundland, 1962–66.

Area[a]	Monthly mean temp (C)	Group no.	Date of capture	No. examined	% with new shells	% ready to molt	Carapace[b] length range (mm)
			Port au Port Bay				
	Surface						
May	5.7						
June	9.7						
July	13.0						
Aug.	15.4						
Sept.	14.1	1	Sept. 21, 1962	32	100	0	86–103
Oct.	8.4	2	Oct. 13, 1964	142	93	0	71–108
Nov.	3.6						
			North Arm Bay of Islands				
	6 m depth						
June	8.4						
July	12.5	3	July 30, 1965	21	5	0	58–81
Aug.	16.1	4	Aug. 26, 1965	96	85	1	68–90
Sept.	14.4						
Oct.	9.0	5	Oct. 1, 1965	155	90	0	60–93
Nov.	4.6	6	Oct. 30, 1965	95	98	0	59–91
			Port aux Choix				
	Surface						
June	8.3						
July	13.2	7	July 18, 1966	40	0	0	51–92
Aug.	15.8	8	Aug. 16, 1966	43	84	2	47–102
		9	Aug. 31, 1966	50	90	4	63–98
Total examined				674			

[a]Depths ranged from 6 to 14 m; bottom temperatures would be approximately equal to surface temperatures.

[b]Measured from the base of the eye socket to rear margin of the carapace.

but subjected to several different kinds of stress situations. A significant reduction in the molting incidence after mild treatment is illustrated in Table II.

Further evidence of the inhibition of the molting process by restrictive procedures is given in Table III and Table IV. Chi-square analyses (two way classification method, Dixon and Massey, 1951) performed on these data and summarized in Table V, aided in determining the relative importance of the various factors as inhibitors of the molting process. Table V illustrates that even mild conditions of captivity (individual cages; groups 15 and 17) inhibit molting significantly. When the effects of tagging or marking are superimposed upon the effects of captivity (groups 13, 14, and 16) the inhibitory

TABLE II. Per cent of molting observed in male lobsters which had been marked and released the previous year.

Group no.	Locality of capture	Days in captivity	Date of release	No. released	Date of recapture	Tag	No. recaptured and examined	Carapace[a] length range (*mm*)	No. molted	% molted
10	Bay of Islands	7–21	June 22–24, 1964	695	May 1–July 1, 1965	Dart	37	71–88	11	30
11	Bay of Islands	7–21	July 6, 1963	514	May 1–July 1, 1964	Tail fan bored	60	72–106	41	68
12	Port au Port Bay	3–14	July 9, 1962	568	May 1–July 1, 1963	Tail fan bored	108	83–118	75	69

[a]Pre-ecdysal carapace lengths.

TABLE III. Molting incidence in western Newfoundland male lobsters after treatment.

Group no.	Locality of capture	Date of capture	Treatment	Days in captivity	Date of final examination	Tag	No. examined	Carapace[a] length range (*mm*)	No. molting	% molted
13	Lark Hr., Bay of Islands	July 20, 1964	Held 2 days, then caged singly at 5 m depth, fed weekly on scallop gonad and mantle	83	Oct. 11, 1964	Dart	4	65–82	1	25
14	Lark Hr., Bay of Islands	July 20, 1964	"	83	Oct. 11, 1964	Tail fan bored	7	68–83	2	29
15	North Arm, Bay of Islands	July 28, 1965	Held 1 day, then caged singly at 7 m depth, fed weekly on scallop gonad and mantle	65	Sept. 30, 1965	None	8	76–86	3	37
16	North Arm, Bay of Islands	July 28, 1965	"	65	Sept. 30, 1965	Ferro-magnetic tag	13	77–88	3	23
17	Port aux Choix	July 21, 1966	"	72	Sept. 29, 1966	None	28	61–92	14	50

[a]Pre-ecdysal carapace lengths.

TABLE IV. Molting incidence of adult male Fourchu[a] lobsters held in captivity[b] under highly restricted conditions which enforced a high degree of association.

No. under observation	Group no.	Illumination (*lumens/ft²*)	Food[c]	No. molted	% molted
July 26–Dec. 17, 1964					
50	18	40	+	12	24
48	19	24	+	12	25
25	20	8	+	5	20
50	21	0	+	10	20
50	22	40	–	11	22
49	23	24	–	11	22.4
50	24	8	–	12	24
48	25	0	–	6	12.5
Total 370				79	21.3

[a]Average pre-ecdysal carapace length, 90 mm.
[b]Temperatures for this period are illustrated in Fig. 2.
[c]Herring and beef liver ad libitum.

TABLE V. Chi-square values for lobster-molting incidences.

Lobster groups	Treatment	Observed chi-square value	Theoretical chi-square value
2+5+9 vs. 18–25	Free vs. highly restricted but untagged	356.3	$X^2_{99.5}$ 7.88
2+5+9 vs. 10+11+12	Free vs. tagged or marked and released	52.45	
2+5+9 vs. 11+12	Free vs. released after tail fans bored	39.79	
15+17 vs. 9+4	Mildly restricted but untagged vs. free	21.92	
10 vs. 11	Dart tagged vs. bored tail fan	13.59	
18–25 vs. 15+17	Highly restricted, untagged vs. mildly restricted, untagged	12.78	
17 vs. 9	Mildly restricted, untagged group showing the higher molting incidence vs. free	11.09	
18+19+20+22+23+24 vs. 15+17	Highly restricted, untagged in light vs. mildly restricted, untagged	9.38	
13+14+16 vs. 15+17	Tagged and mildly restricted vs. mildly restricted but untagged	3.0	X^2_{95} 3.84
22+23+24 vs. 25	Highly restricted, untagged starved: light vs. darkness	2.45	X^2_{90} 2.71
21 vs. 25	Highly restricted, untagged darkness: food vs. starvation	1.78	

effect is increased. The data for group 10 (Table II) suggest that tagging alone could reduce molting significantly; however, a larger experiment should be carried out to determine whether this apparent effect is real. A molting inhibition equivalent to or even greater than that produced by tagging and mild captivity could be achieved by highly restrictive conditions which enforce a high degree of association between lobsters (groups 18–25, see Tables IV and V). Handling of lobsters is probably an inhibitory factor which contributed in part to all of these effects; however, it was not treated as a separate variable in these experiments.

Mortalities among the captive lobsters did not play a part in our experiments; only two deaths not related to cannibalism of a molting lobster occurred among the 370 lobsters listed in Table IV. Presumably the individual shelters gave sufficient protection to keep mortalities of pre-ecdysal lobsters at a low level.

Darkness, moderate temperatures, and solitude have been listed by Bliss and Boyer (1964) as factors which favor the onset of pro-ecdysis in the land crab, *Gecarcinus lateralis*. Certainly solitude appears to be a favorable factor for lobster molting, but the influence of light is not as clear-cut. Darkness, under the highly restricted and crowded conditions, did not result in a higher molting incidence for the fed lobsters (Table IV); instead its sole effect appeared to be an inhibition of the molting of starved losbters. The observed χ^2 value (2.45) for group 25 vs. the combined groups 22, 23, and 24 closely approaches the theoretical χ^2_{90} value of 2.71 (Table V). The other light intensities apparently had no effect on molting incidences.

Donahue (1954) suggested that the duration and intensity of illumination could be important in stimulating ecdysis in *H. americanus* and Stephens (1955), in fact, has shown such an effect using the crayfish *Cambarus* (*Orconectes*) *virilis*. When the crayfish kept at a constant temperature (15 C) were exposed to daily and increasing periods of illumination, they molted more frequently. Mortalities not related to molting, however, increased similarly. Our results were obtained using a constant period of illumination; a varied program with other light intensities or continuous (24 hr) illumination may have produced greater effects. We are not ruling out light as a factor in lobster molting, but believe that the unfavorable environmental conditions existing in these experiments could have negated any stimulatory effect. Twenty per cent of the lobsters molting under highly restricted conditions (groups 18–25) did so during the night. This nocturnal molting was distributed evenly through all of these groups.

The types of tags or marks used in these experiments are designed to be applied to the lobster prior to ecdysis and be detectable afterwards. Tags or marks are used in field studies to acquire information on size increases per molt, molting incidence, and migration patterns. The assumption made is that the tags or marks do not interfere significantly with the life patterns of the lobster and that data acquired through the use of tags or marks are equally applicable to untagged animals. Thus the indications that tagging or the

handling incidental to tagging interferes with at least one aspect of the lobster's life assumes a high degree of practical importance.

Preliminary data on the effect of marking lobsters by boring holes in the tail fan (group 14, Table III) suggest this procedure initially is highly inhibitory to molting. There are indications, however, that lobsters can overcome much of this effect eventually (see groups 11 and 12, Table II). One group of 568 male lobsters (group 12) captured in the Port au Port region in July 1962 were marked by boring holes in the tail fan and released. The following July, 108 of this group were recaptured; 69% had molted. A similar experiment was conducted in the Bay of Islands with 514 male lobsters (group 11) captured in July 1963 and released after holes were bored in their tail fans. Sixty were recaptured the following July; 68% had molted. Wilder (1953) using this technique recorded molting incidences ranging upwards from 77%. The data on tagging and marking indicate that an assessment of the effects of (*a*) duration and form of captivity and handling prior to tagging and release and (*b*) the effects of the particular tag or mark should be made prior to its use.

The influence of temperature on molting was shown for lobsters at Grande-Rivière, Quebec (Corrivault and Tremblay, 1948) and its influence is broadly apparent in Table I. The temperatures which the Newfoundland lobsters (Tables I, II, and III) experienced are roughly equal to those for the Nova Scotia lobsters (Table IV, Fig. 2). A high molting frequency is apparent in

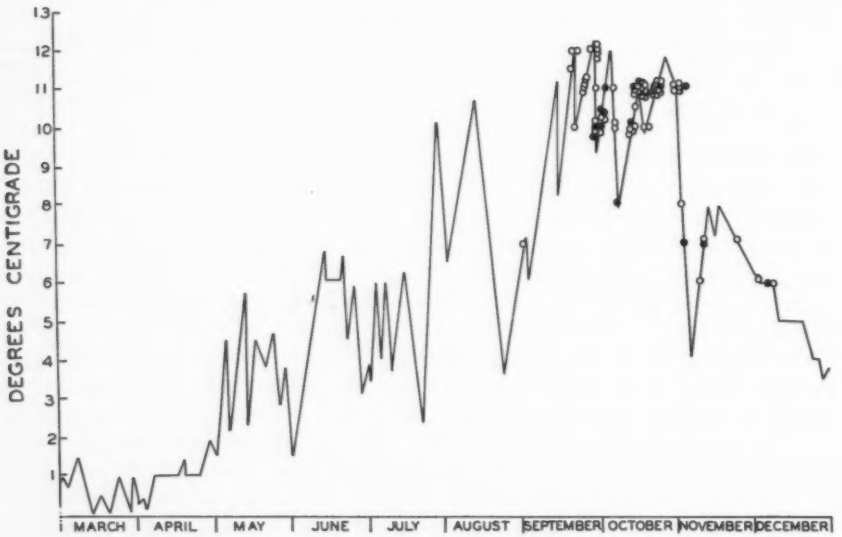

FIG. 2. Molting incidence for lobsters (groups 18–25) plotted on temperature curve for the ambient seawater temperatures in the aquarium prior to and during the course of the experiments (equivalent to both Halifax and Fourchu temperatures) maintained by pumping external sea water through the aquarium (two complete changes per hour). ○ = lobsters exposed to light; ● = lobsters kept in darkness.

Fig. 2 after the start of the warm-water period, followed by a lower frequency with the onset of the colder winter water temperatures. Presumably, for the lobsters, the warmer water period prior to molting is necessary for entry into pro-ecdysis as Passano (1960a) suggested was the case for the crab *Uca pugnax*. The late molting of a few lobsters (between 8 and 6 C) substantiates Passano's (1960a) suggestion that pro-ecdysis is prolonged but not necessarily halted by lower temperatures. Additional proof of this was provided after the termination of the experiment in mid-December. Approximately 100 lobsters from groups 18–25 were retained in the aquarium; one molted on January 6 at 3 C and another on January 26 at 1 C.

The diets used in these experiments did not appear to be significant factors in the molting process. The groups permitted a natural diet (groups 10, 11, and 12), scallop gonads and mantles (groups 13–17), beef liver and herring (groups 18–21), or starvation (groups 22–24) all suffered a high degree of molt inhibition. Only starvation coupled with darkness seemed to have any additional effect on molting (group 25) and even that was an enhanced negative effect. Thomas (1965) suggests that for *Nephrops norvegicus* sparse feeding results in a reduced growth increment rather than molt inhibition. Passano (1960a), however, speculated that for *Uca pugnax* kept at high temperatures (20–30 C) food is extremely important for the mobilization of the necessary hepatopancreatic reserves; and Dall (1965) showed that for animals such as *Metapenaeus* sp., whose reserves are slight, molting is adversely affected by a lack of food.

The lobster, since it can draw on all of its body components (Stewart et al., 1967b), has relatively immense reserves. Although molting in the lobster could be affected by specific diets, the large reserves should keep the dietary effects to a low level. The extent of the lobsters' reserves, and proof that highly diminished reserves were not actually harmful to the lobsters, was illustrated by the low mortality rates for groups 22–25 and for lobsters starved even more extensively (Stewart et al., 1967a).

It is possible that some of the factors such as the effect of the various tags and marks or some forms of captivity and handling could be overcome with time. Hughes and Matthiessen (1962) showed that the molting of adult, hatchery-reared lobsters kept in separate tanks is not inhibited, whereas the effect of crowding a cannibalistic animal such as *H. americanus* presumably violates its innate territorial instincts and perhaps cannot be overcome easily. A partial explanation for molt inhibition may be that the temperatures of the waters discussed in this report are just high enough to permit molting under good conditions; adverse conditions of any sort could inhibit the pro-ecdysal development sufficiently to prevent ecdysis. Evidence suggesting that the balance between molting and nonmolting is extremely delicate has been presented by Stewart and Li (1968). A reasonable conclusion is that any stress situation would be expected to delay or inhibit ecdysis, thereby supporting the contention of Herrick (1911) and Passano (1960b), who regard molting as a product of central nervous system stimulation.

In this discussion we have drawn a number of comparisons between our data for lobsters and that for other crustaceans. It should be remembered, however, that the different crustacean genera appear to vary greatly in their response to various stimuli; consequently, generalizations based upon results obtained with one genus have definite limitations.

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Morphometrics, Distribution, Growth, and Maturity of Offshore Sand Launce (*Ammodytes dubius*) on the Nova Scotia Banks[1]

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ABSTRACT

A population of *Ammodytes dubius* occurs on the Nova Scotia banks, the fish being much larger than those reported previously for the species. The ranges of vertebral and anal fin ray numbers for *A. dubius* are extended. Research records of the launce, from catches and from stomach contents of predators, indicate that it is widely distributed over the banks throughout the year, but is concentrated in depths of 20–50 fath. Maturity data show that it is a winter spawner. A tentative growth curve, based on age–length determinations using otoliths, indicates that the growth pattern is similar to that of *A. lanceolatus*. The launce is shown to be an important item in the diet of cod and a constituent, in the egg or the adult stage, in the diets of many other commercially exploited fishes of the Nova Scotia banks.

INTRODUCTION

The sand launces (*Ammodytes* spp.) are considered to be among the great unexploited fish resources of the northwest Atlantic[2] and important food items in the diet of the commercially valuable food fishes of the Nova Scotia and Newfoundland banks. In spite of this, little is known of their abundance, distribution, or biology in the area.

The inshore launce, *A. hexapterus* Pallas, 1831 (= *A. americanus* DeKay, 1842) has been recorded from various localities along the Nova Scotia coast but apart from two records, one of post-larvae in 1885 and one of "older specimens" in 1870 (Richards et al., 1963), there were no specific records of the offshore launce, *A. dubius* Reinhardt, 1838, from Nova Scotia to Cape Cod until 1967. (Prior to this date, sand launce caught on the Nova Scotia banks by Canadian commercial and research vessels were incidental to catches of other fishes and were not identified to species.) The gap in the distribution records for identified *A. dubius* was filled only during Fisheries Research Board research cruises in 1967. As a result of efforts made specifically for capture of sand launce, considerable numbers of a launce with meristic counts characteristic of *A. dubius* were trawled on Emerald and Western banks. The population is exceptional in that the fish grow to a much greater size than has previously been recorded for the species. It is rivalled in size among the launces by only the European *A. lanceolatus* Le Sauvage, 1824 which has distinctive specific characters. Analysis of the Nova Scotia material provides

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new data on the meristics, morphometrics, growth, breeding season and distribution of the population.

There is considerable difference of opinion about the taxonomic status of the different groups of North American *Ammodytes*. For the purposes of the present paper the grouping of Richards et al. (1963) is accepted, and there are considered to be two species, *A. dubius* and *A. hexapterus*. In addition, *A. marinus* (Raitt, 1934) is recorded from West Greenland where there is a complex relationship between it and *A. dubius* (Einarsson, 1951).

MATERIAL AND METHODS

All Nova Scotia specimens of offshore sand launce examined in 1967 were taken on Emerald and Western banks in a #36 or #41 Yankee trawl with a codend liner of 0.5-inch mesh. This captured fish down to 12.7 cm long. Large samples were examined immediately after capture for length and sex data and subsamples were quick-frozen or preserved in alcohol for later laboratory examination. In addition, a sample of 39 *A. dubius* from West Greenland was used to obtain comparative data on meristic numbers.

Age estimations were made from otoliths. Only those with well-defined annuli were used, representing 273 fish out of 412 examined. Vertebral (158), anal fin ray (309), and dorsal fin ray (315) counts were made by dissection and direct observation. Measurements of 1175 fish were taken as total length to the nearest millimetre in fresh material except when standard lengths were required for morphometric comparison. Fish which had been frozen or preserved in alcohol were measured separately and their lengths adjusted to those of fresh specimens by comparison of the length-frequency distribution curves for fresh and preserved specimens from the same sample.

Sex and maturity data were collected from 786 fish. Maturity was determined according to the scale: 1 — immature, resting, or recovering; 2 — ripening; 3 — ripe; 4 — spawning; 5 — spent (Macer, 1966).

The distribution of sand launce on the banks from 1956–67 was estimated by examination of (*a*) 71 catch records of sand launce by research vessels; and (*b*) 524 records from research vessels of sand launce in the stomach contents of principal fish species (Table III) together with the relevant data on position, date, bottom temperature, and depth at capture of the fish concerned. It is assumed for determination of distribution, and also for computation of percentage volumes of the total stomach contents of cod and haddock contributed by sand launce, that all specimens recorded from the offshore Nova Scotia banks are of the same species.

In using the stomach contents records it is necessary to assume that the fish in which the launce were found had not moved far, either in distance or in depth, since eating its prey. This is a reasonable assumption from what is known of movements and feeding habits of the fish concerned, and from the fact that to be identifiable under working conditions at sea, when the records were taken, the launce would have to be little-digested and, therefore, very recently ingested.

MERISTICS AND MORPHOMETRICS

On the basis of vertebral (V), dorsal fin ray (D), and anal fin ray (A) numbers (Table I), the Nova Scotia material obviously fits into the *A. dubius* group. The maximum dorsal and anal fin ray numbers for the Nova Scotia material (D = 69; A = 36) exceed those previously recorded for *A. dubius* (D = 68; A = 35) (Richards et al., 1963) and thus extend the known ranges for the species.

TABLE I. Meristic numbers for Canadian and West Greenland sand launces.

Species or population	No. in sample	Range	Mean
Vertebrae			
A. americanus (Backus, 1957)	13	62–69	67.2±1.67[a]
A. dubius — Nova Scotia	146	71–78	74.6±1.23
A. dubius — Labrador (Backus, 1957)	13	71–75	73.2±1.48
A. dubius — West Greenland	39	73–78	75.03±1.11
A. marinus — (Raitt, 1934)	205	67–72	69.21±1.13
Anal fin rays			
A. americanus (Backus, 1957)	11	28–31	29.6±0.98
A. dubius — Nova Scotia	257	31–36	33.3±0.95
A. dubius — Labrador (Backus, 1957)	13	32–35	32.9±1.07
A. dubius — West Greenland	39	32–36	33.4±0.97
A. marinus — (Raitt, 1934)	205	28–33	30.61±1.09
Dorsal fin rays			
A. americanus (Backus, 1957)	11	57–60	58.5±0.99
A. dubius — Nova Scotia	265	61–69	64.2±1.28
A. dubius — Labrador (Backus, 1957)	13	62–67	64.5±1.69
A. dubius — West Greenland	38	62–67	64.8±1.49
A. dubius — (Raitt, 1934)	205	56–62	59.1±1.20

[a]Standard deviation of mean.

The Nova Scotia material had mean vertebral and anal fin ray numbers as high as the Labrador material. This is in contrast to the general trend of increasing meristic numbers with increasing latitudes in *A. dubius* (Richards et al., 1963). This may be due to the small size of the Labrador sample (13 specimens) or to some anomaly in the gradient of the factor(s) which determine the meristic numbers. The exceptional size of the Nova Scotia fish supports the latter alternative.

Richards et al. (1963) have dealt exhaustively with the morphometrics of *A. dubius*. They regard the ratio of body depth:standard length as the "most important morphometric criterion for separation of the two groups of sand launces along the American coast." In the *A. dubius* group the ratio, expressed as a percentage, ranges from 6.8 to 9.2 whereas for *A. hexapterus* the range is 7.1–9.7. In the Nova Scotia material the range from a subsample

of 20 specimens was 7.9–9.3 and although it is slightly higher than the *A. dubius* range given by Richards et al., it is not so different that it casts any doubt on the identification of the Nova Scotia material from analysis of meristic numbers.

The length of the sand launce in the northwest Atlantic is stated by Richards et al. to range from 4 to 9 inches (10.2–22.9 cm) along the North American east coast, no distinction being made between *A. dubius* and *A. hexapterus* in this respect. Leim and Scott (1966) give the greatest length of *A. hexapterus* (= *A. americanus*) as 8½ inches (21.6 cm) and that of *A. dubius* as 8 inches (20.3 cm). The greatest total length noted in the Nova Scotia material, so far, is 37.2 cm, i.e. some 80% greater than the previously recorded upper limit of total length for *A. dubius*. The lengths in samples (236 specimens) taken on Emerald Bank in July–August 1967 ranged from 13.4 to 37.2 cm with a mean length of 23.3 cm and the highest peak in the length-frequency distribution at 28 cm (Fig. 1).

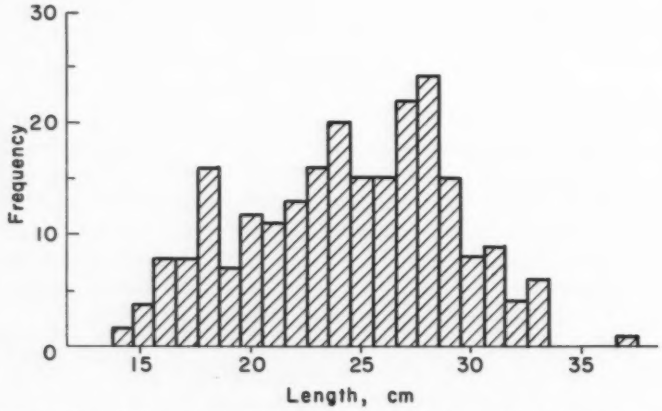

FIG. 1. Length-frequency distribution of *A. dubius* (149 specimens) on Nova Scotia banks (July–August 1967).

The large size of the fish in the Nova Scotia population is rivalled among the launces by *A. lanceolatus* only. The latter is readily distinguished from *A. dubius* by its toothed vomer, however, and is a summer spawner. No launce with toothed vomer has been recorded from the northwest Atlantic. The significance of the large size of the Nova Scotia *A. dubius* and the relationships between the populations of the large launce and neighbouring populations of smaller launce have yet to be determined. *Ammodytes* exhibits great intraspecific variation and it is possible that relatively minor differences in the environment may result in morphometric differences which would be of great significance in other fishes but which are of little specific significance in *Ammodytes*.

AGE–LENGTH RELATIONSHIPS

An age–length curve for the launce was constructed from the mean lengths of the fish at estimated ages (Fig. 2), using otoliths with well-defined annuli.

Since the samples used are distributed from May to November 1967 and the fish spawn mainly in December–January (see below), the weighted mean length of each year-class sample is assumed to represent the length

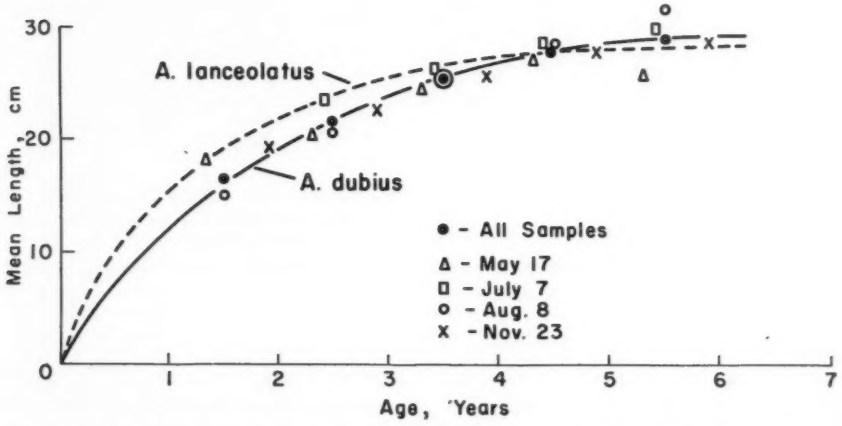

FIG. 2. Growth curves for *A. dubius* (273 specimens) and *A. lanceolatus*. The points on which the curve for *A. lanceolatus* is based (Macer, 1966) are omitted.

half-way through the year, i.e., at $1\frac{1}{2}$, $2\frac{1}{2}$, $3\frac{1}{2}$ years, etc. The curve approximates that of *A. lanceolatus* (Macer, 1966), which grows to a similar size, but indicates that the Nova Scotia *A. dubius* has a slightly lower growth rate although it approaches a similar asymptotic length.

BREEDING SEASON

Data on the maturity of Nova Scotia *A. dubius* at different times in 1967–68 (Table II) indicate that the launce breeds on the offshore Nova Scotia banks in winter, commencing in late November. Spawning reached its peak in December–January and ended before March.

Further evidence of winter spawning was provided by the presence of large numbers of sand launce eggs, in late stages of development, in the stomach contents of yellowtail flounders (*Limanda ferruginea*) on Western Bank on January 23, 1967 and February 12, 1968.

The percentages of each sex in different stages of maturity (Table II) indicate that there is little difference in rate of development between the two sexes although the male matures at a slightly earlier date than the female.

The maturity data indicate that the Nova Scotia *A. dubius* has a fairly short and well-defined winter breeding season. It differs slightly from the

TABLE II. Seasonal changes in percentages of male and female *A. dubius* in different stages of maturity on Nova Scotia banks (1967–68).

Date	No. of specimens	Sex	Immature, resting, or recovering	Ripening	Ripe	Spawning	Spent
1967							
May 19	156	♂	43.9	51.0	–	–	5.1
		♀	48.4	41.3	1.7	–	8.6
July 7	99	♂	5.7	92.4	–	–	1.9
		♀	2.1	93.6	4.3	–	–
Aug. 8[a]	50	♂	–	100	–	–	–
		♀	–	100	–	–	–
Nov. 23	212	♂	–	–	46.2	52.8	1.0
		♀	–	–	98.0	1.0	1.0
1968							
Feb. 12	17	♂	12.5	–	–	–	87.5
		♀	14.3	–	–	–	85.7

[a]This sample had been preserved in alcohol and the maturity was estimated from the size of the gonads.

West Greenland *A. marinus*, which breeds in early spring (Einarsson, 1951), but more so from the West Greenland *A. dubius*, which breeds in early summer (Einarsson, 1951), and *A. hexapterus*, a summer spawner. These differences in breeding season may be of no significance in regards to separating species (Miller, 1961) but, in accordance with Quasim's (1955) conclusions from the spawning seasons of other marine teleosts, the difference in breeding season of *A. dubius* between Greenland and Nova Scotia suggests that the Nova Scotia banks are near the southern limit of the distribution of the species.

In the samples obtained from the spawning stocks of the launce in November 1967 even the smallest fish taken (18–20 cm) were mature, at an estimated $1\frac{3}{4}$ years old. The difficulty of distinguishing between immature, resting, and recovering fish has already been indicated but in the sample taken in May 1967, 40% of the specimens under 20 cm long, i.e., in the 1+ age-group, were classed as immature rather than fish which had spawned. This, in conjunction with the sample mentioned above, suggests that the fish mature in their 2nd year.

IMPORTANCE AS A FOOD SPECIES

The records of launce in stomach contents of predators (Table III) indicate that the sand launce is of some importance as a food species for other fishes throughout the year, including some of the most important commercial groundfish of the Nova Scotia banks. No cruises have been made in December, hence the lack of records for that month.

The degree of importance of the launce to the cod and haddock stocks of the Scotian Shelf is shown in an analysis of the stomach contents of these

TABLE III. Predators in the stomach contents of which sand launce were found, by month, in FRB research cruises 1956–57.

Predator	Month											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Atlantic cod (*Gadus morhua*)	×	×	×	×	×	×	×	×	×	×	×	
Haddock (*Melanogrammus aeglefinus*)		×	×	×	×	×	×	×	×	×		
White hake (*Urophycis tenuis*)			×			×						
Pollock (*Pollachius virens*)	×	×	×	×	×		×	×		×		
Redfish (*Sebastes marinus*)							×					
Atlantic halibut (*Hippoglossus hippoglossus*)			×	×	×					×		
American plaice (*Hippoglossoides platessoides*)		×	×	×		×	×		×			
Witch flounder (*Glyptocephalus cynoglossus*)							×					
Yellowtail flounder (*Limanda ferruginea*)	×		×				×		×			
Atlantic wolffish (*Anarhichas lupus*)				×								
Atlantic herring (*Clupea harengus*)							×					
Thorny skate (*Raja radiata*)		×	×	×			×	×		×		
Smooth skate (*Raja senta*)						×	×					
Winter skate (*Raja ocellata*)		×		×		×	×					
Spiny dogfish (*Squalus acanthias*)						×						
Longhorn sculpin (*Myoxocephalus octodecemspinosus*)							×			×		

fishes (Tables IV and V). The percentage by volume of sand launce in the diet of Atlantic cod ranges up to 50% (in large cod) of the total volume of food recorded. It is a relatively minor item in haddock diet, ranging up to 4%. In both cases its importance increases with the size of the fish and with their movement into shallow water. These figures do not reflect the importance

TABLE IV. Volumes of sand launce in stomachs (percentages of total contents) of cod of various lengths from two depths in first quarter of years 1958–63 in three areas off Nova Scotia (FRB research cruise data). Number of fish examined in parentheses.

Area	Depth (*fath*)	Length of cod (*cm*)			
		0–29	30–49	50–69	70+
Sable Island	0–49	(252) 4.7	(310)47.6	(500)76.1	(323)75.9
	50+	(216) 4.2	(378) 1.5	(427) 1.5	(335) 3.4
Banquereau	0–49	(30)18.0	(98)22.5	(123)11.5	(91)18.1
	50+	(153) 0.0	(386) 2.0	(329) 1.4	(157) 2.8
N.E. Cape Breton	0–49	(50) 0.0	(100) 0.0	(74) 0.0	(18) 0.0
	50+	(149) 0.0	(466) 0.0	(523) 0.0	(402) 0.0

TABLE V. Volumes of sand launce in stomachs (percentages of total contents) of haddock of various lengths from two depths in Sable Island area at different seasons (FRB cruise data 1958–63). Number of fish examined in parentheses.

Season	Depth (*fath*)	Length of haddock (*cm*)		
		0–29	30–39	40+
Jan.–Mar.	0–49	(110) 0.0	(66) 0.9	(182)20.7
	50+	(349) 0.0	(387) 0.0	(721) 0.1
Apr.-June	0–49	(74) 0.0	(169) 4.7	(1023)16.7
	50+	(392) 0.0	(423) 0.2	(958) 0.3
July–Sept.	0–49	(189) 2.4	(601) 1.2	(729)16.3
	50+	(305) 0.0	(225) 0.0	(257) 0.0

of the larvae and eggs of the sand launce in the diet of many of the fishes of the area. It has been mentioned above that eggs were found in the stomachs of yellowtail flounder and the enormous abundance of sand launce larvae in the area (Serebryakov, 1965) suggests that, as in Europe (Raitt, 1934), the eggs and larvae are vital factors in sustaining the stocks of many of the Nova Scotia fishes at their present levels.

DISTRIBUTION

The positions in which sand launce were (*a*) caught or (*b*) found in stomach contents of other fishes in 1956–67 are distributed widely over the Nova Scotia banks (Fig. 3) and are limited to the banks. Apart from Emerald Bank, where tows were made specifically for sand launce, the records were incidental

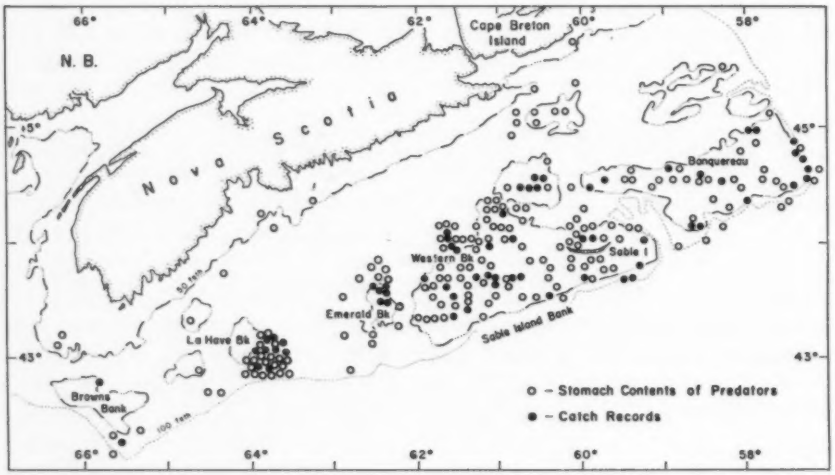

FIG. 3. Records of sand launce from Nova Scotia banks (FRB research cruises 1956–67).

to work on other species of fish and the distribution therefore reflects the interests of scientists in these other species rather than a uniform spread of effort over the whole of the area. This is well illustrated in the area of LaHave Bank where there was a concentration of effort on cod and haddock in depths between 50 and 100 fath. The grouping of the records just off the top of the bank does not mean that there are no sand launce in the shallower water. Emerald Bank illustrates a situation where there are no records of sand launce in the stomachs of fish taken on top of the bank although there are concentrations of sand launce in this area, as shown in FRB cruise records for July and November 1967, when comparatively large catches were made (up to 10,000 specimens per $\frac{1}{2}$-hr tow).

The average number of fish caught per tow and average number of records of launce in stomach contents of predators per tow vary with depth and temperature (Fig. 4A, B). Most of the launce occur at temperatures from 0 to 6 C and at depths between 20 and 50 fath. The catch data are erratic and are biased by the results of a few efforts specially aimed at catching sand launce. The stomach-contents records, although they reflect special interest in a few of the main commercial fishes, are on a much wider basis and are considered to give a better picture of the distribution in relation to temperature and depth. They indicate that there is not such a high degree of temperature selectivity as there is of depth selectivity. This is confirmed by the occurrence of the launce throughout the year on the banks (Table III), which suggests that they are eurythermal.

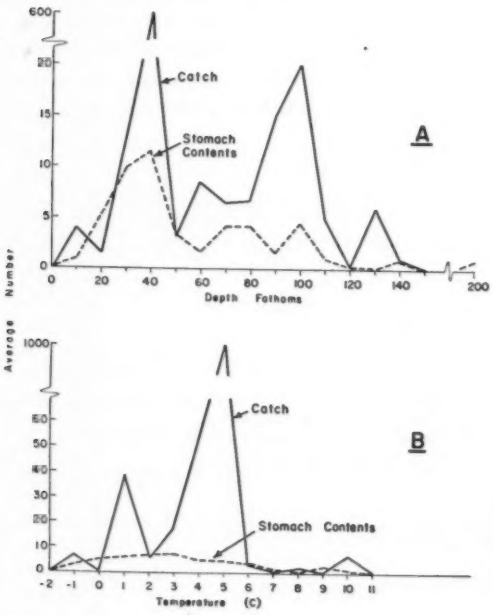

FIG. 4. Average numbers per tow of sand launce caught and of records of sand launce in stomach contents of predators by (A) depth and (B) temperature (FRB research cruise data 1956–67).

The fact that large catches of launce were made in 1967 on exactly the same area on Emerald Bank in both summer (July) and winter (November) suggests that there is little seasonal movement of the stocks, if any, but the occasional reports from commercial fishermen of the appearance of large concentrations in some areas may result from seasonal movements or, on a long-term basis, from undetermined hydrographical factors.

The records indicate that the launce occur over the whole of the Nova Scotia banks. The heaviest concentrations appear to be in the central part of the area, tailing off to the northeast and possibly the southwest, although commercial fishermen report dense shoals on Browns Bank at times. The diminution of the stocks to the northeast is reflected in the greater importance of sand launce in the diet of cod in the LaHave–Sable Island banks as compared with the Banquereau area (Table IV).

Catch data indicate that localised concentration is the case with adult *A. dubius* on the banks. They are widely distributed but, in spite of widespread trawling on numerous research cruises covering most of the Scotian Shelf, large numbers have seldom been caught. The heavy catches on Emerald Bank in 1967 were made in a very limited area, and the catch rate declined sharply outside this area. Some caution is therefore required in predicting the size of the stocks and their economic potential on the basis of larval abundance or occasional large hauls of adults. Separate, localised populations could quickly be reduced by intensive fishing and in view of the importance of the launce to the cod (Table IV) and other fishes, heavy exploitation of the launce for fish meal or fish protein concentrate, which is already being considered, might well have an adverse effect on the stocks of cod and other food fishes. Conversely, continued depletion of the proportion of large fish in the cod population on the banks, as has taken place in recent years, may ead to an increase in the sand launce stocks as a result of reduced predation.

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Reproduction in Brook Trout (*Salvelinus fontinalis*) Fed Sublethal Concentrations of DDT[1,2]

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ABSTRACT

When sexually maturing yearling brook trout were fed for 156 days with DDT at rates that evidently caused no mortality, fish fed at the lower dosages produced more mature ova than untreated fish. Those fed at the highest dosage produced fewer mature ova than untreated fish. The size of the male fish at the end of the feeding period tended to increase according to dosage of DDT. In eggs and sac fry obtained from various mating combinations of gametes from the experimental groups, mortality was with one exception higher when at least one of the gametes came from treated fish than when they both came from untreated fish. A major portion of the mortality of sac fry in groups where the eggs came from treated fish occurred during the 15th week of development. This period coincided with the period of maximum utilization of yolk fat reported to occur in other salmonid fry, and indicated that insecticide residues in the eggs were released at this time and resulted in the observed mortality. The residue concentrations in the fish at the end of the feeding period were similar to those reported for wild fish.

INTRODUCTION

Recent reports have described the widespread occurrence, in aquatic habitats, of persistent organochlorine insecticides in quantities below the levels acutely toxic to aquatic life (Welch and Spindler, 1964; Weaver et al., 1965; Lauer et al., 1966). To understand the impact on fish populations of chronic exposure to such sublethal levels it is necessary to evaluate not merely the ability of the organisms to survive but also their ability to carry out reproduction and other fundamental life processes. This investigation was concerned with the effects of chronic exposure to DDT on the size and number of mature ova produced by brook trout (*Salvelinus fontinalis*), the potency of their gametes, and the viability of their eggs and sac fry.

Previous investigators concerned with chronic exposure of fish to sublethal concentrations of insecticides have demonstrated effects only on survivors of concentrations lethal to a portion of the population (Mount, 1962; Allison et al., 1964; Andrews et al., 1966). There is considerable doubt whether the term sublethal accurately describes such effects or concentrations. As suggested by Sutherland et al. (1967), studies on sublethal effects of insecticides should be based on dosages sublethal to the entire population. This report describes such an investigation.

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[2]Based on a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy from the University of New Hampshire, Durham, N.H.

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MATERIALS AND METHODS

A group of 280 yearling brook trout, with a mean weight of 162 g, was provided by the New Hampshire Fish and Game Department. These fish were randomly divided into four experimental groups and held in rectangular outdoor raceway pens. One of these groups (control) was fed untreated feed, which was found to contain 0.36 ppm DDT, a concentration equivalent to a dosage of 0.05 mg/kg per week. The other groups were fed DDT at the rates of 0.5, 1.0, and 2.0 mg/kg per week, respectively, for a period of 156 days, from June 2 to November 7, 1966. Technical grade DDT (77.7% *p,p'* DDT) was incorporated into the diet by dissolving it in acetone and mixing this with corn oil (Table I). Analysis of the dry pelleted feed indicated that 90–95% of the calculated dosage was achieved by this method. Feeding was

TABLE I. Formula[a] for the dry pelleted diet fed to yearling brook trout (*Salvelinus fontinalis*).

Ingredient	% total feed
Fishmeal	40.0
Distiller's solubles	18.5
Wheat Middlings	10.0
Brewer's yeast	10.0
Glucose	7.0
Alfalfa meal	5.0
Corn oil	3.0
Dicalcium phosphate	2.5
Cellulose	2.0
Choline–chloride	1.25
Vitamin mix	0.50
Trace mineral mix	0.25
Total protein — 37.60%	
Total calculated energy — 2586 cal/kg	
Calorie/protein ratio — 34:1	

[a]This formula was provided by Dr R. C. Ringrose, Department of Animal Sciences, University of New Hampshire, Durham, N.H.

twice daily, 6 days per week, at 65% of the rate recommended for moist feed and brook trout by Deuel et al. (1952). Fish were fed half of the weekly dosage on the 1st and 4th days of each week by mixing DDT-treated feed (never less than 80% of the total daily ration) with untreated feed. All groups were fed untreated pellets for 10 days before the experiment began to insure satisfactory acceptance of the pellets. The stability of the pellets in water, and the rapidity with which they were consumed, suggested that most of the calculated dosage was delivered.

The experiment was conducted at the New Hampshire Fish and Game Department Rearing Station in New Durham, N.H. The characteristics

of the water at this station during the experimental period were: temperature, 2–18 C; *p*H, 7.4–7.6; dissolved oxygen, 8.0–12.6 ppm; free carbon dioxide, 1.0–2.0 ppm; total alkalinity as $CaCO_3$, 11.2–14.0 ppm.

To study the effects of the insecticide on the potency of the gametes and the viability of the eggs and fry, eggs were stripped from 21 females on November 9, 1966. These were fertilized according to the following schedule:

Mating combination:	C-O	S-1	S-2	E-S-1	E-S-2	E-1	E-2
DDT fed female parent (*mg/kg per week*)	0.0[a]	0.0	0.0	1.0	2.0	1.0	2.0
DDT fed male parent (*mg/kg per week*)	0.0	1.0	2.0	1.0	2.0	0.0	0.0

[a]Untreated feed contained 0.36 ppm DDT (equivalent to 0.05 mg/kg per week).

Because of the limited facilities available, no gametes from the group receiving the lowest DDT dosage were utilized in producing fertilized eggs. For each mating combination three pair of fish were stripped. After water hardening, the fertilized eggs were transfered to the State Fish Hatchery in New Hampton, N.H., where they were incubated on egg trays at a temperature of 7 ± 1 C until hatching. The sac fry were held until the feeding stage, at which time they were fixed in Bouin's solution and preserved for residue analysis. Dead fertilized eggs and sac fry were removed twice weekly and the mortality was recorded. Fertilization was determined by examining coagulated eggs cleared with a 2.0% NaCl solution.

To study the effects of DDT on the number of mature ova produced, yearling females, not stripped, were weighed, measured, and killed. The eggs were removed, weighed, and preserved in Davidson's solution according to the method described by Henderson (1963). Eggs from each fish were counted directly and the mean egg diameters were determined according to the method of Vladykov (1956).

No mortality attributable to DDT occurred during the period of exposure, and all of the brook trout were sexually mature at the end of this period. During the 1st week of the experiment, 11 fish were lost as a result of natural predation. The use of wire screens over the raceway prevented the recurrence of such mortality.

The weights and lengths of the fish were analyzed for differences due to the insecticide treatments. Analysis of variance, using a method for unequal subclass sizes (Steel and Torrie, 1960), tested for main effects of insecticide dosage and sex, as well as for interaction between main effects. Multiple covariance analysis (Steel and Torrie, 1960), using fish weight in grams (X_1) and mean egg diameter in millimeters (X_2) as the independent variables, tested for differences due to DDT in the number of mature ova produced (Y). Differences between means were tested for statistical significance using Duncan's multiple range test as modified for unequal subclass numbers by Kramer (1956). The adjusted mean number of mature ova produced was calculated using the regression coefficients, as well as the mean weight of

female brook trout and the mean diameter of eggs in each experimental group. The chi-square test for differences in egg and fry mortality among mating combinations, and individual degree of freedom comparisons, were conducted using the methods described for binomial populations by Li (1964). All statistical differences were accepted at $P = 0.05$.

Whole fish samples from the control group and the higher dosage groups, along with fish samples taken before the experiment began, were frozen for analysis. These along with samples of gonads and eggs from these same groups, and feed samples, were sent to the Wisconsin Alumni Research Foundation for residue analysis. For fish, eggs, and gonads, dried samples were ground with sodium sulfate and extracted in a Soxhlet apparatus with a mixture of 70 ml ethyl ether and 170 ml petroleum ether for 8 hr. After extraction the ethers were removed by evaporation on a steam bath. The sample was redissolved in petroleum ether and washed onto a Florisil column. Pesticides were eluted from the column with 5–95% and 15–85% ethyl ether–petroleum ether solutions. The respective solutions were taken to near dryness, and a known volume was injected into a Barber–Colman Pesticide Analyzer, Model 5360, equipped with an electron capture detector. Feed samples were extracted with acetonitrile. After filtering off the solids, the acetonitrile was diluted with water and the solution extracted with hexane.

Sac fry were analyzed at the Fish-Pesticide Research Laboratory in Columbia, Mo. Samples were extracted with 10% diethyl ether in petroleum ether. Clean-up involved partitioning with acetonitrile, followed by treatment with fuming sulfuric acid. Analysis was completed using a Varian Aerograph Model 200 gas chromatograph equipped with electron capture.

RESULTS

The differences in weight among the experimental groups or between the sexes were not significant. However, at the end of the feeding period, the males were significantly longer than the females; among the males those receiving the highest dosage were significantly longer than those in the control (Table II). The interaction between insecticide dosage and sex was not significant. The differences in mean egg diameters among the experimental groups (Table III) were not significant.

The number of mature ova produced was related to the size of the fish and the mean egg diameter. The regression equation was

$$\hat{Y} = \bar{y} + 3.13x_1 + 749.9x_2.$$

Multiple covariance analysis indicated that there were significant differences in the numbers of mature ova produced after adjusting for fish weight and egg size. The fish fed the lower dosages contained more, and the fish fed the highest dosage contained fewer, mature ova than did fish in the control group (Table III).

TABLE II. Mean fork lengths and weights of yearling brook trout at the end of the feeding period.

Rate of feeding DDT (*mg/kg per week*)	Sex	No. of fish	Fork length (*mm*)	Weight (g)
0.0[a]	Male	30	298.5(2.9)[b]	332.8(5.1)
	Female	22	302.9(3.2)	377.0(5.9)
	Combined	52	300.2(2.1)	351.5(3.8)
0.5	Male	23	307.1(3.2)	377.2(5.8)
	Female	28	300.3(2.8)	383.3(5.2)
	Combined	51	303.2(2.1)	380.5(3.8)
1.0	Male	24	307.4(3.1)	384.2(5.6)
	Female	34	306.3(2.6)	400.1(4.7)
	Combined	58	306.7(1.9)	393.7(3.6)
2.0	Male	27	311.4(2.8)[c]	401.1(4.7)
	Female	26	297.8(2.8)	365.9(5.4)
	Combined	53	304.4(2.1)	383.8(3.8)

[a]Untreated feed contained 0.36 ppm DDT (equivalent to 0.05 mg/kg per week).
[b]Standard error.
[c]Significantly different from the control group at $P = 0.05$.

TABLE III. Mean sizes and numbers of mature ova taken from 89 female brook trout at the end of the feeding period.

Rate of feeding DDT (*mg/kg per week*)	Diam	Eggs/fish (unadjusted)	Eggs/fish (adjusted)[a]
0.0[b]	3.803(.06)[c]	1636(81.3)[c]	1590(10.6)[c]
0.5	3.861(.05)	1694(55.4)	1711(7.7)[d]
1.0	3.860(.05)	1664(55.4)	1733(7.2)[d]
2.0	3.796(.07)	1596(65.5)	1510(9.3)[d]

[a]Adjusted for fish weight and egg size.
[b]Untreated feed contained 0.36 ppm DDT (equivalent to 0.05 mg/kg per week).
[c]Standard error.
[d]Significantly different from the control group at $P = 0.05$.

The treatments appeared to have little effect on the viability of the gametes. The mean percent fertilization was 63.1 with a range among the different mating combinations of 58.0–69.2%. Fertilized eggs were all eyed by the 48th day, and hatched between the 64–70th day.

The cumulative mortality of fertilized eggs and fry to the swim-up stage was higher when one or both of the gametes were from a DDT-treated fish than when both gametes were from control fish (Fig. 1). Individual degree of freedom comparisons indicated that mortality in all of the mating combinations, except S-2, was significantly higher than that in the control. Considerable mortality occurred during the 7th week, at which time the eggs were addled. The cumulative mortality curves follow one of two general

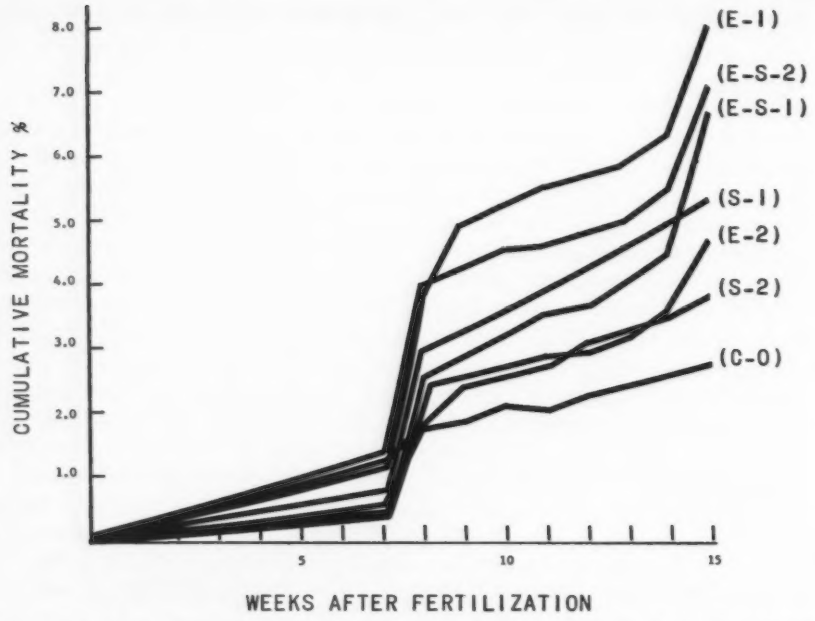

FIG. 1. Cumulative mortalities of eggs and sac fry, from fertilization to the feeding stage, of brook trout fed DDT at various rates for 156 days. C-O, both parents untreated; S-1, male parent fed at 1.0 mg/kg per week; S-2, male parent, 2.0; E-S-1, both parents fed at 1.0 mg/kg per week; E-S-2, both parents, 2.0; E-1, female parent fed at 1.0 mg/kg per week; E-2, female parent, 2.0. Each curve is based on the combined data for all of the eggs and fry representing each mating combination. Untreated feed contained 0.36 ppm DDT (equivalent to 0.05 mg/kg per week).

patterns. The slope is either relatively constant after the 8th week or increases markedly after the 14th week.

Except for residues found in fish testes from groups receiving the higher dosage rates, the amounts of total residues in whole adult brook trout and in eggs and testes at the end of the exposure period were directly related to the levels of exposure (Table IV). The total residues found in sac fry 15 weeks after hatching were directly related to the dosage received by the female parent. The total residue concentration in pretreatment samples was 0.31 ppm; the slightly higher concentration in untreated fish at the end of the exposure period was the result of the occurrence of DDT in one or more of the feed ingredients.

DISCUSSION

The lack of mortality among brook trout during exposure to DDT contrasts with the mortality reported for cutthroat trout (*Salmo clarki lewisi*) fed similar dosages of DDT by Allison et al. (1964). They reported that after 5 months of feeding DDT, cumulative mortality in the group fed 3.0 mg/kg per week was greater than 60%, and in the group fed 1.0 mg/kg per week it was greater than

TABLE IV. Concentrations of residues (ppm) found in whole bodies, testes, and eggs of brook trout after being fed DDT at various rates for 156 days, and in their fry at the swim-up stage.

Rate of feeding DDT (*mg/kg per week*)		Whole fish			Eggs			Testes			Fry		
Males	Females	(DDE)	(DDD)	(DDT)[b]	(DDE)	(DDD)	(DDT)[b]	(DDE)	(DDD)	(DDT)[b]	(DDE)	(DDD)	(DDT)[b]
0.0[a]	0.0[a]	0.34	0.26	0.18	0.05	–	0.16	0.03	0.01	0.03	0.04	0.11	0.34
0.0	0.0	0.18	0.13	0.09	0.05	–	0.14	0.01	0.01	0.02	–	–	–
1.0	1.0	0.60	1.10	1.30	0.13	–	0.76	0.08	–	0.46	–	–	–
1.0	1.0	0.40	1.00	1.40	0.19	–	2.22	0.11	–	0.64	–	–	–
1.0	1.0	–	–	–	0.20	–	1.15	0.05	–	0.28	–	–	–
2.0	2.0	0.80	3.50	3.30	0.23	–	3.00	0.09	–	0.50	0.67	0.26	1.89
2.0	2.0	1.10	3.00	3.50	0.26	–	2.40	0.08	–	0.58	0.94	0.41	2.80
2.0	2.0	–	–	–	0.29	–	4.74	0.07	–	0.33	–	–	–
2.0	0.0	–	–	–	–	–	–	–	–	–	0.11	0.05	0.16
2.0	0.0	–	–	–	–	–	–	–	–	–	0.07	0.02	0.11
0.0	2.0	–	–	–	–	–	–	–	–	–	0.84	0.28	1.50
0.0	2.0	–	–	–	–	–	–	–	–	–	1.03	0.30	1.76

[a]Untreated feed contained 0.36 ppm DDT (equivalent to 0.05 mg/kg per week).
[b]Values for DDT represent both *o,p* and *p,p* DDT.

30%. One possible explanation of this difference is that different species were involved. Schoenthal (1963) reported that brook trout were less susceptible to DDT than cutthroat trout during short-term exposures. However, the difference in susceptibility to DDT between the species does not seem to be great enough to explain the complete lack of mortality among the brook trout. A more probable explanation of this difference lies in the methods used in delivering the weekly dosage. In the cutthroat trout study (Allison et al., 1964) the fish received the entire weekly dosage on the 1st day of the week, whereas the brook trout received half the weekly dosage at 3-day intervals. It is possible that the fish were capable of more efficiently metabolizing small amounts of DDT given frequently than large amounts given less frequently. If this were the case, toxicity might be less under the former conditions of exposure than the latter, although the same dosage is involved.

My data (Table II) indicate that male fish from the treated groups tended to be longer than control males. Although no significant differences in weight were indicated, a definite trend, indicative of a relationship between dosage rate and size of male fish at the end of the exposure period, was evident. A similar trend was reported for cutthroat trout exposed to DDT by Allison et al. (1964). These authors suggested that this apparent increase in size was a possible indirect effect of DDT because of mortality of small, diseased, slow-growing fish in the treated lots. Since there was no mortality among the brook trout after the first week of the exposure period, the apparent differences in the size of the male brook trout among the experimental lots may

indicate a direct effect on growth due to exposure to DDT. Why the trends appear to be more pronounced in the males than the females is another matter for speculation. The exposure of these fish to DDT occurred for 5 months prior to spawning, a period when developing eggs undergo a three to four-fold increase in size. Based on the mean levels of DDT residues found in whole fish and eggs, and on the mean weights of fish and eggs, I calculated that approximately 14–18% of the total residues in female brook trout from the higher dosage groups were found in the eggs. Assuming that the trend to differences in the size of male brook trout indicated a real effect of the insecticide on growth, it is possible that, during this period, enough of the insecticide was stored in the eggs to preclude any effect of the DDT on growth in female brook trout.

Differences in the number of mature ova produced due to insecticide exposure have not been previously reported. Allison et al. (1964) reported that no differences were evident in the number of eggs produced by cutthroat trout exposed experimentally to DDT. However, these authors did not take into account the influence of egg size and fish weight on egg number. It is possible that variation in egg size and fish weight masked actual differences in egg number, as it might have in this investigation since analysis of variance of raw data (unadjusted Y) indicated no significant differences in number of mature ova resulted from insecticide exposure.

Burdick et al. (1964) reported that complete losses of lake trout (*Salvelinus namaycush*) sac fry were positively correlated with the DDT content of the egg. Since data are not available on the mortality of the adults in the wild populations from which these eggs were obtained, it was impossible to determine whether or not effects of sublethal concentrations were described. The effects of DDT on developing brook trout sac fry are in general agreement with those reported in the lake trout study, with one notable exception. Burdick et al. (1964) suggested that male lake trout did not contribute to the mortality of the sac fry. However, cumulative mortality data for brook trout fry in groups where only the male parent was exposed to DDT (Fig. 1) suggested that the sperm from treated males may affect survival among fry. Reproductive failure in males can result from lack of motility, a decrease in volume, or a biochemical deficiency in the semen. The percent fertilization achieved with sperm from treated males was similar to that of controls and indicates motility probably was not affected. Histological examination of testes, as well as comparison of maturity indices of treated and control males, indicated that the volume of sperm was not appreciably decreased. Therefore, if the mortality in groups of fry where only the sperm came from a treated parent represents a real effect of the insecticide, it may be due to a biochemical change. Cruea[4] (personal communication) has found a significant decrease in the calcium content and total protein of the seminal plasma of cutthroat trout exposed to endrin.

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[4]Darrel Cruea, formerly Physiologist, U.S. Bureau of Sport Fisheries and Wildlife, Fish-Pesticide Research Laboratory, Columbia, Mo.

In groups where the eggs were from DDT-treated fish, a rapid increase of sac fry mortality occurred, as in the lake trout study, just before the fry were ready to feed. That such an increase did not occur in matings where the eggs were from untreated fish suggests that the insecticide in the eggs from treated fish caused the mortality among the sac fry at this time. The time of this increased mortality corresponded with the period of development in other salmonids during which utilization of yolk fat has been reported (Hayes, 1949) to be most rapid. If the brook trout and the other salmonids are similar in timing of rapid utilization of yolk fat, the observed mortality may be due to release of insecticide residues from the fat.

Burdick et al. (1964) indicated that a concentration of 10 ppm DDT or more in lake trout eggs produced 50% or greater mortality of fry; 4.75 ppm or more usually resulted in at least 15% mortality. The levels of DDT in eggs from DDT-exposed brook trout were somewhat less than 4.75 ppm. Based on the lake trout study, these levels would produce somewhat less than 15% mortality among brook trout sac fry. This is exactly what occurred. Also, the DDT residues found in the female brook trout at the end of the exposure period were similar to those found in apparently healthy trout from natural waters in areas sprayed with DDT for insect control (Cope et al., 1958; Schoenthal, 1963; Welch and Spindler, 1964). Such findings indicate that reductions of trout fry populations could be occurring in some of our natural waters as a result of persistent contamination by DDT.

Regarding insecticide pollution, no-effect levels rather than no-kill levels must serve as the basis for establishing water quality criteria. It is only by determining the more subtle responses of fish to sublethal levels of insecticides that such no-effect levels can be established. Among the type of observations that may eventually be used to this end are those changes in reproductive potential described in this report.

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Rates of Accumulation of ^{14}C-Dieldrin Residues in Tissues of Goldfish Exposed to a Single Sublethal Dose of ^{14}C-Aldrin[1]

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ABSTRACT

Immediately after goldfish (*Carassius auratus* (Linnaeus)) had been exposed for 8 hr in a static system to 0.05 ppm of ^{14}C-aldrin, ^{14}C-dieldrin was detected in various tissues. The percentages that were dieldrin increased with time in all of the tissue studied until at 32 days they were 93.9% or more except for visceral fat. Except in visceral fat, 50 and 100% of the residues were dieldrin within 2.5–5.4 and 31.5–92.4 days respectively. For visceral fat the corresponding times were 46.9 and 14,733 days.

INTRODUCTION

There is virtually no information in the literature indicating how rapidly dieldrin appears in the tissues of fish which have been exposed to aldrin. In fact, the available information on this subject might be interpreted to mean that the epoxidation of aldrin to dieldrin occurs slowly or not at all in fish.

The purpose of this study was to investigate the rates at which dieldrin residues accumulate in the tissues of goldfish which have been exposed to aldrin. Boyle et al. (1966) reported that aldrin was converted to dieldrin in the muscle and viscera of fish which had been exposed to aldrin for 22 days, but, when death occurred within 5 days after a massive dose, conversion was very slight. Chan et al. (1967) compared the epoxidation of aldrin in preparations of trout and rat liver microsomes and reported that trout liver microsomes had comparatively little ability to epoxidize aldrin to dieldrin.

According to the data of Henderson et al. (1959), dieldrin is slightly more toxic to fish than aldrin is. The 24-hr median tolerance limits of four species of freshwater fish ranged from 0.089 to 0.018 ppm for aldrin and from 0.062 to 0.014 ppm for dieldrin in soft water. Therefore, the conversion of aldrin residues to dieldrin within fish could not be considered a detoxification reaction.

METHODS

Forty goldfish, averaging 27.8 g in weight, were exposed to 0.05 ppm of ^{14}C-aldrin (specific activity 1.17 mc/mM) for 8 hr. During the exposure severe symptoms of toxicity were observed, but no deaths occurred then or during the following 32-day period. After the exposure, the fish were transferred to a recovery aquarium continuously flushed with noncontaminated water at

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the rate of 2 liters/min. Samples, each consisting of five fish, were taken immediately after the exposure was terminated and seven more times (Table I) during the 32 days. The water temperature during recovery was 21 ± 1 C.

Equivalent amounts of individual tissues from each of the five fish in a sample were pooled for analysis. This, in effect, averaged the results of a five-fish sample. After the tissues were removed from the fish they were dissolved in formic acid at 60 C and then the formic acid–tissue solution was extracted four times with an equal volume of hexane. The four hexane extracts for each tissue were combined and evaporated over a steam bath and the residue was redissolved in acetonitrile. Approximately 500 mg of adsorption alumina was slurried with the acetonitrile, and the mixture was then centrifuged at 10,000 × *g* for 10 min. The supernatant was decanted into a clean centrifuge tube and the acetonitrile evaporated over a steam bath. The final residue was dissolved in either benzene for gas chromatography or ethyl acetate for thin-layer chromatography. The total ^{14}C-aldrin and ^{14}C-dieldrin content of each sample was determined by measuring the ^{14}C-activity in a 100-μliter subsample of either the benzene or ethyl acetate solution. These determinations were made by liquid scintillation and count efficiencies were determined by the internal standard method.

For all tissues except the lateral line nerve and spinal cord, the aldrin and dieldrin concentrations were determined by electron-capture gas chromatography. Compounds present in the lateral line nerve and spinal cord and apparently not removed by the clean-up procedure interfered with the

TABLE I. Total concentrations of ^{14}C-aldrin plus ^{14}C-dieldrin (expressed as ppm ^{14}C-aldrin) in goldfish tissues at various times after exposure of the fish to ^{14}C-aldrin. The time scale originates at the beginning of the exposure, and the first sample (0.33 days) was taken immediately after the exposure was terminated.

	Days after beginning 8-hr exposure to ^{14}C-aldrin							
Tissue	0.33	0.83	1.33	2.33	4.33	8.33	17.33	32.33
Blood	2.12	1.50	1.13	0.99	0.69	0.69	0.61	0.40
Brain	5.45	4.40	3.68	3.88	3.26	3.23	2.52	2.30
Visceral fat	–	25.40	–	–	35.90	54.50	–	–
Gall bladder	1.71	2.64	1.50	5.36	2.08	2.17	1.94	0.97
Gills	3.06	2.12	1.61	1.33	1.76	1.49	1.09	0.55
Intestine and stomach	5.96	5.50	4.54	3.53	3.90	3.98	1.87	1.95
Kidney	3.97	3.14	2.50	–	1.90	2.10	1.32	0.92
Liver	4.82	3.36	1.96	1.77	1.98	1.58	1.22	1.62
Muscle	1.70	0.97	0.86	0.58	0.70	0.58	0.52	0.33
Nerve cord	8.95	13.71	7.00	21.60	10.60	7.40	6.76	4.56
Ovary	2.53	2.56	1.55	1.36	1.11	0.80	0.97	–
Skin	4.47	4.10	4.29	3.54	4.08	4.54	2.75	1.53
Spinal cord	–	6.87	4.13	3.76	3.19	2.73	3.22	1.91
Testes	7.16	7.31	3.09	10.42	–	3.54	57.70	2.43

aldrin and dieldrin peaks obtained from the gas chromatograph. Therefore, the percentages of aldrin and dieldrin in these tissues were determined by thin-layer chromatography (Kovacs, 1963) followed by zonal scanning (Snyder and Stephens, 1962). The zonal scanning technique consisted of scraping sequential 8-mm strips of the adsorbant layer from the completed thin-layer plates. These strips were taken perpendicular to the direction in which the solvent traveled. The scrapings of each strip were placed in glass scintillation vials with 2 ml of water, 1 ml of ethanol, and 10 ml of Dioxane Scintillation Cocktail. The relative amounts of radioactivity in the strips corresponding to the aldrin and dieldrin spots were determined by liquid-scintillation counting and from these figures the percentages of aldrin and dieldrin in the lateral line nerve and spinal cord were calculated.

For a given tissue, an approximately linear relationship existed between the per cent of dieldrin in the tissue and the common logarithm of the time after the beginning of the exposure. The least squares method was used to determine the slope and intercept for each set of data for the general equation

$$Y = a + bx$$

where Y is the percent dieldrin existing in the tissue, X is the common logarithm of the time after the beginning of the exposure, a is the intercept, and b is the slope. Using this equation, as determined for each tissue, estimates were made of the times required to attain residues of 50 and 100% dieldrin in each tissue.

Before exposure to ^{14}C-aldrin solution, the fish did not contain measurable quantities of aldrin or dieldrin. Analysis of a hexane extract of the exposure water, after exposure, did not demonstrate detectable quantities of ^{14}C-dieldrin.

RESULTS

The total insecticide concentration (aldrin plus dieldrin) immediately after exposure ranged from 1.70 ppm in the muscle to 8.95 ppm in the lateral line nerve (Table I). The total concentration of aldrin plus dieldrin in each of the tissues decreased, in general, during the 32 days after the exposure, although there were marked fluctuations for some of the tissues. A previous study (Gakstatter, MS, 1966) suggested that the concentrations of chlorinated insecticides in muscle and blood fluctuate less than concentrations in other tissues. If the losses from these two tissues are calculated from the concentrations in Table I, they are 81.1 and 80.6% respectively for blood and muscle. Similar calculations for other tissues give values as low as a 49% decrease so we can assume that between 49 and 82% of the total insecticide initially present in the fish was lost during the 32-day recovery.

Immediately after the exposure of the fish to aldrin, dieldrin was detected in the tissues. At this first sampling, the percentage of the total residue that was dieldrin ranged from 1.1% for the blood to 20.7% for the lateral line nerve; however, for all tissues except the lateral line nerve and the gall bladder

TABLE II. Percentages of the total residues in goldfish tissues which were ^{14}C-dieldrin at various times after beginning of exposure of the fish to ^{14}C-aldrin.

	Days after beginning 8-hr exposure							
Tissue	0.33	0.83	1.33	2.33	4.33	8.44	17.33	32.33
Blood	1.1	24.9	34.1	56.9	58.9	78.6	83.1	95
Brain	6.9	–	33.1	40.9	48.6	63.2	73.3	95.6[a]
Visceral fat	–	14.7	–	–	30.1	34.4	–	–
Gall bladder	20.4	–	21.4	44.0	39.4	71.2	71.9	95
Gills	7.1	16.4	25.6	45.4	47.6	69.1	72.3	95
Intestine and stomach	5.6	23.0	25.6	43.8	39.0	77.9	71.4	95
Kidney	6.3	22.1	26.0	–	48.9	77.4	79.8	95
Liver	8.1	28.6	34.6	50.6	35.9	73.6	80.9	95
Muscle	7.9	27.8	25.3	43.0	45.8	78.3	71.8	95
Nerve cord	20.7[a]	22.1[a]	38.5[a]	44.3[a]	–	84.4[a]	79.6[a]	93.9[a]
Ovary	6.6	25.5	20.1	32.9	45.5	76.8	75.0	–
Skin	8.7	19.8	26.4	33.6	36.3	56.4	68.1	95
Spinal cord	–	10.8[a]	29.1[a]	49.5[a]	56.0[a]	63.5[a]	77.0[a]	96.1[a]
Testes	3.7	17.4	17.4	38.0	–	59.5	70.2	95

[a]Values determined by thin-layer chromatography followed by zonal scanning.

TABLE III. Estimated numbers of days required, after beginning of exposure of the fish to ^{14}C-aldrin, for the residues in each tissue to consist of 50 and 100% ^{14}C-dieldrin. These estimates were made from linear regression equations calculated from the data in Table II.

	Days	
Tissue	50% ^{14}C-dieldrin	100% ^{14}C-dieldrin
Lateral line nerve	2.5	42 2
Blood	2.8	31.5
Liver	3.2	49.6
Kidney	3.4	41.8
Muscle	3.5	51.7
Gall bladder	3.7	71.8
Brain	3.8	58.5
Intestine and stomach	3.8	52.2
Spinal cord	3.8	41.8
Gills	3.9	53.1
Ovary	4.1	57.7
Testes	4.7	61.2
Skin	5.4	92.4
Visceral fat	46.9	14,733.0

the values were 8.7% or less (Table II). The percentages that were dieldrin increased with time in all of the tissues until at 32 days they were 93.9% or more except for visceral fat.

The estimated times required for the dieldrin residues to reach 50 and 100% of the total residues were 2.5–5.4 and 31.5–92.4 days respectively for all tissues except visceral fat (Table III). For visceral fat the corresponding times were 46.9 and 14,733 days.

DISCUSSION

The pattern of distribution of residues of aldrin plus dieldrin in the goldfish tissues is similar to that previously reported by Gakstatter (MS, 1966) in tissues of several species of freshwater fish after exposure to the chlorinated insecticides dieldrin, DDT, and lindane. These insecticides are found in all tissues, but the greatest concentrations occur in fat depots, whereas the lowest concentrations are almost invariably in the muscle and blood of the fish.

This was not intended to be a definitive study on the rate of epoxidation of aldrin to dieldrin by goldfish because other factors are obviously involved. The results, however, indicate that goldfish do have the capability of epoxidizing aldrin and that substantial portions of aldrin residues in their tissues are converted to dieldrin within a few days. Since it is not known whether aldrin and dieldrin are excreted by fish at the same rate, the actual epoxidation of aldrin may proceed at a faster or slower rate than the results of this study indicated.

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Caloric Content of the Standing Crop of Benthic and Epibenthic Invertebrates of St. Margaret's Bay, Nova Scotia[1,2]

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ABSTRACT

The benthos of St. Margaret's Bay at depths of 28–62 m was sampled quantitatively during the summer and the caloric contents of the common invertebrates determined. The shrimps, amphipods, and the polychaete *Lumbrinereis* with caloric contents between 1000 and 1300 cal/g wet weight had the highest caloric content of those tested. The mean caloric content of the standing crop was 76 kcal/m^2 with the highest values occurring where the sand and silt–clay fractions of the sediment were nearly equal and the lowest where either sand or silt–clay predominated. Annelids and echinoderms together accounted for more than three-quarters of the caloric content of the standing crop.

INTRODUCTION

St. Margaret's Bay on the coast of Nova Scotia with an area of 130 km^2 is enclosed by land on all sides except for a 5.5-km opening to the Atlantic on the south. The bay, because of its enclosed nature, was chosen as the site for a study of the processes controlling the productivity of marine communities, and this paper describes the results of a survey of the benthic invertebrate community in the bay. By measuring the biomass of bottom invertebrates larger than 0.5 mm sampled quantitatively by a grab, and determining the caloric contents of all the common species found, it was possible to estimate the amount of food energy per square meter of seabed. All stations sampled were chosen to lie below the thermocline. The resulting similarity in temperature, salinity, and depth allowed the results to be analysed for the effect of sediment type on the total calories per square meter found.

The study was also undertaken to determine the difference in caloric content between species within the same phylum and whether seasonal changes in the caloric contents of these invertebrates were all in the same direction. Differences between caloric contents of species and phyla reflect their value as sources of food energy for predators such as fish, some of which feed heavily on bottom fauna.

MATERIAL AND METHODS

The invertebrates for determination of caloric content were collected from June to October 1966 and in March and April 1967 by grab and beam

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trawl from the bottom of St. Margaret's Bay, at a depth of 25 m or more. Live, undamaged individuals were weighed after removing surface water with absorbent towelling giving a live weight which included the weight of food in the intestine. This method was chosen as fish using these invertebrates as food would also ingest the contents of the invertebrates's intestine and because determinations of biomass of invertebrates present in the bay was based on these total weights. Shells were removed from molluscs after their live weight had been determined and large invertebrates such as holothurians were cut into small strips. All animals were dried to constant weight in a forced draft oven at 75 C and powdered to pass through a 20-mesh sieve. Approximately 1-g samples were combusted in a Parr adiabatic oxygen bomb calorimeter following the method given in the Parr manual (Parr Instrument Co, 1964). After each combustion the acid and fuse wire corrections were determined. In addition it was found that the sulphur content of the samples exceeded 0.1% so a sulphur correction was required. The sulphur content was determined by a conductometric titration of the bomb washings against barium acetate as suggested by Barthel et al. (1950). It was found necessary to dilute the bomb washings to 500 ml and allow 4 min for the acetate reaction to take place after each addition of 0.25 ml of 0.1 N barium acetate to get consistent readings.

The carbonate content of the dry material from echinoderms was determined by adding excess HCl to a known amount of material and collecting the generated CO_2 quantitatively with a CO_2 absorbent. Assuming all carbonate to be $CaCO_3$ and applying the correction of 0.137 cal/mg $CaCO_3$ given by Paine (1966) allowed a correction for endothermy to be applied to this group. It was not possible to combust brittlestar material and this may be explained by its 81% carbonate content.

The caloric contents of one 22-cm herring and one 14-cm cunner, *Tautogolabrus adspersus*, were determined to provide values against which the food energy of an invertebrate diet could be compared with one consisting largely of fish.

Except where indicated otherwise, caloric values are based on three determinations varying less than 2% from the mean. For molluscs the dry weight excludes the weight of the shell. The caloric value of live molluscs was calculated assuming that the shell had no caloric value but including its weight. All other weights are for entire animals.

At the same season and in the same area from which invertebrates were being collected for caloric determinations quantitative samples of the benthic fauna were taken at 17 stations using a $\frac{1}{10}$-m^2 Van Veen grab. At least five samples were taken at each station and the total wet weight of each species determined. The total number of calories represented by each of the common species could then be calculated. Rarer species for which the caloric content was not known were assigned the mean caloric value for the phylum to which they belonged. From these values the number of calories per square metre and their distribution among the phyla could be calculated for each station.

The total excludes organisms too small to be retained on the 0.5-mm opening screen through which the sediment was washed and epibenthic forms agile enough to avoid the grab.

From 12 of the stations a sediment sample was taken with the grab and analyzed for grain size by wet sieving after treatment with hydrogen peroxide and ammonium hydroxide to remove aggregates. From an echo-sounder survey accompanied by grab samples the boundaries of the main sediment types were established and are shown in Fig. 1. The composition of these sediments may be obtained by referring to the analysis of grain size for stations within each sediment zone given in Table I.

RESULTS

Caloric Content of Benthic Invertebrates

The caloric values obtained (Tables II and III) show that there are considerable differences between species even within the same phylum. All the molluscs without shells, annelids, and arthropods contained between 2000 and 5000 cal/g dry weight whereas echinoderms generally had lower values of 800–3000 cal. On a wet-weight basis differences between the phyla appear. Arthropods, with the exception of *Hyas*, have the highest values being above 1000 cal/g wet weight. The annelids, with one exception, are next with a range of 450–1050 cal. The inclusion of the shell in the wet weight depresses the caloric content of molluscs so that they contain between 350 and 800 cal/g wet weight. The echinoderms had low caloric values on a dry-weight basis and among holothurians this is made still lower on the wet-weight basis by a water content more than two or three times the content of arthropods. The starfish, in contrast, have a low water content and so on a wet-weight basis their caloric content is similar to that of the molluscs and annelids.

The shrimp *Argis dentata* showed a significantly higher caloric content ($p < 0.001$) for egg-bearing females than for other adult shrimp taken in the same haul.

The herring tested, containing 6.6% fat, had 1927 cal/g wet weight and 6360 cal/g dry weight compared with 1058 and 4880 cal respectively for the cunner. Herring and cunner were chosen for testing as representing two extremes among fish, the herring with small skeleton and high oil content and the cunner with heavier skeleton and low in oil. If they do represent the range then it appears that fish contain much more energy per gram than invertebrates, with the exception of crustacea which are comparable in this respect to the cunner.

The collections made in March and April at the time of the lowest bottom water temperatures (0.4 C) and before the first plankton bloom, contained six species which had been collected from the same area in the summer at temperatures of 1.8–2.4 C (Table III). There was no general trend apparent either on a dry- or wet-weight basis when species collected at the two seasons were compared; some species gained whereas others lost caloric value between

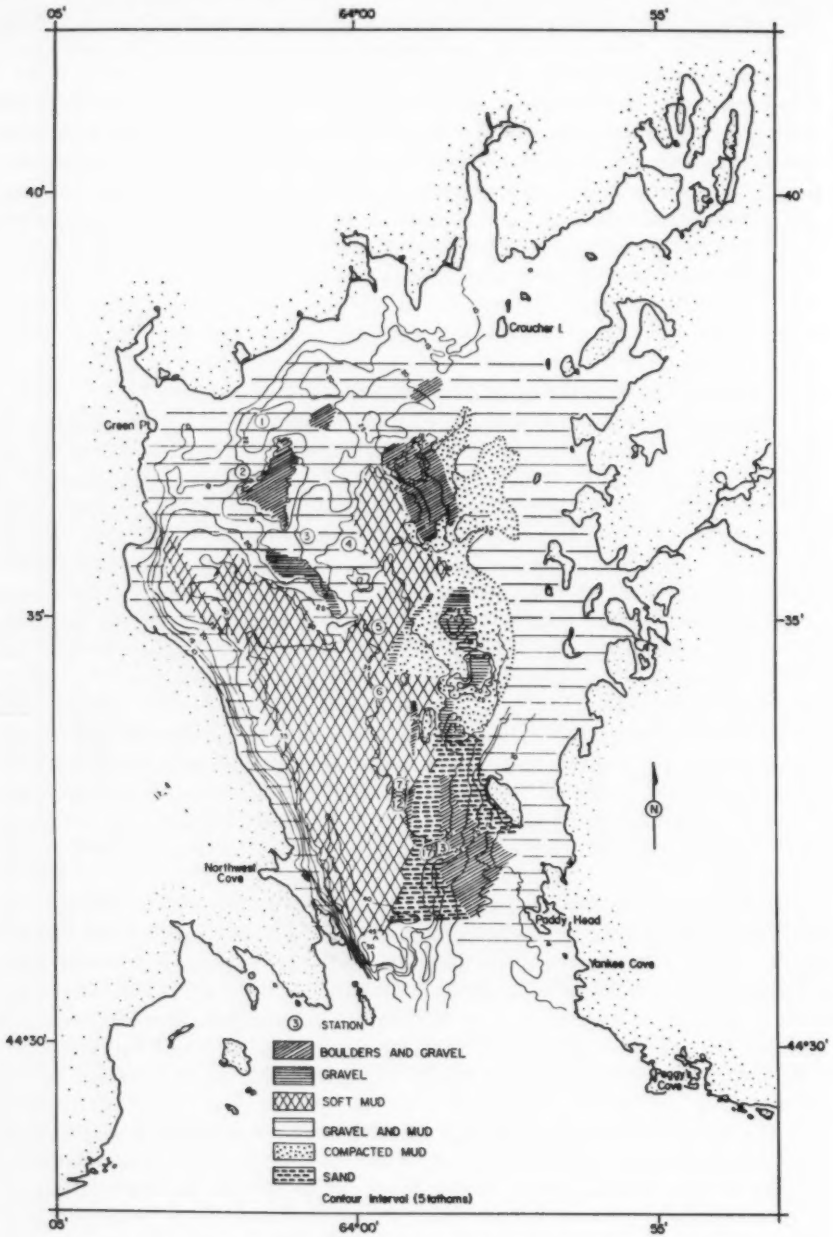

FIG. 1. Location of quantitative sampling stations and sediment types.

TABLE I. Sediment analysis. Each fraction given as a per cent of the sediment by weight.

Station	Gravel + coarse sand >500 μ	Medium sand 500–250 μ	Fine sand 250–105 μ	Very fine sand 105–37 μ	Silt + clay <37 μ
3	0	0	1	4	95
5	0	0	0	3	97
6	0	0	0	6	94
7	0	0	5	41	54
8	3	1	20	24	52
9	0	0	2	25	73
10	0	0	2	25	73
11	0	0	2	26	72
12	0	0	19	55	26
13	0	0	19	64	17
14	0	0	18	61	21
15	0	0	1	23	76

the spring and summer seasons. Since the animals tested did not respond in the same way or to the same extent, it would not be valid to adjust the caloric content of animals determined at one season by a constant amount to arrive at their probable contents at another season.

CALORIC CONTENT OF STANDING CROP

The standing crop of benthic and epibenthic animals as collected by the Van Veen grab at depths of 28–62 m in St. Margaret's Bay during the summer contained on the average 76 kcal/m² (Table IV). The highest value obtained, 174 kcal/m², was from station 8 where the sediment (Table I) contained almost equal amounts of fine sand (44% between 37 and 250 μ) and silt with clay (52% below 37 μ). Fewer calories per square meter were present on sediments containing a preponderance of either sand or silt (Fig. 2). Within the 28–62-m depth range covered there was no evident relationship of caloric abundance to depth.

Of the 17 stations sampled annelids contributed most to the total calories recorded at 8 stations, echinoderms at 7, and molluscs at 2 (Table IV). The common invertebrates chosen for caloric determinations contributed 85% of the total calories present. Only 15% of the total resulted from calculations in which an animal was assigned the mean value for the phylum to which it belonged.

DISCUSSION

The caloric contents of the animals studied have been expressed in terms of wet and dry weights rather than as ash-free dry weight to emphasize the differences caused by varying amounts of inorganic material on the value

TABLE II. Caloric content of invertebrates collected between June and October from St. Margaret's Bay, N.S. Results based on three determinations each.

	Mean individual wt (g)	Cal/g dry wt	Cal/g live wt	Largest deviation from mean (%)	Sulphur in dry material (%)	Live wt equalling 1 g dry wt (g)
Coelenterata						
Duva multiflora[a]	29.2	2886	494	0	1.0	5.8
Annelida						
Lumbrinereis fragilis	2.7	4857	1059	0.7	2.6	4.6
Terebellids	0.3	4141	805	0.6	1.3	5.1
Nepthys ciliata	6.5	4061	747	0.7	1.1	5.4
Aphrodita hastata	40.3	3438	486	1.0	1.5	7.1
Phascolion strombi[a]	0.3	3389	595	0.3	0.7	5.7
Maldanids (*Axiothella*, *Niochamache*)	–	3276	653	0.3	1.3	5.0
Pectinaria hypoborea	0.4	3242	624	1.2	0.9	5.2
Pherusa plumosa	0.7	2660	463	1.4	0.8	5.7
Sternapsis fossor	0.2	2127	538	0.8	0.9	4.0
Arthropoda						
Argis dentata ♀ with eggs	4.3	4878	1158	0.4	0.7	4.2
Argis dentata, mixed adults	4.6	4549	1081	0.3	0.7	4.2
Pandalus montagui	2.2	4740	1320	1.0	0.7	3.6
Amphipods	0.5	3761	1058	0.6	0.6	3.6
Mollusca[b]						
Yoldia thraciaeformis	15.4	4783	509	0.5	1.5	9.4
Yoldia sapotilla	1.1	4778	688	0.4	1.2	8.0
Thais lapillus[a,c]	1.6	4595	442	0.9	1.5	5.6
Clinocardium ciliatum	8.8	4453	374	1.2	1.7	11.9
Natica clausa[a]	1.8	4392	791	0.1	1.5	5.6
Scaphander punctostriatus	3.9	3336	418	0.9	2.2	10.4
Echinodermata — with $CaCO_3$ correction						
Cucumaria frondosa	473.0	3073	224	1.6	1.6	13.7
Chirodota laevis[a]	33.3	2569	264	0.5	1.2	9.7
Asterias vulgaris[c]	3.7	2551	633	0.8	0.9	4.0
Ctenodiscus crispatus	26.5	1828	608	0.9	1.1	3.0
Molpadia oolitica[a]	35.5	1554	114	0.8	1.1	13.6

[a]Based on two determinations.
[b]Dry weight of molluscs excludes the shell.
[c]From Bedford Basin.

of various animals as food. Using such caloric values it is possible to determine approximately the caloric content of various fish diets. For example, when in the life history of a fish such as a cod, the diet changes from mainly invertebrate to mainly fish does this result in a richer diet or is the change advantageous for some other reason such as having food in larger units? The composition

TABLE III. Caloric content of invertebrates collected in March and April 1967 from St. Margaret's Bay, N.S.

	Mean individual wt (g)	Cal/g dry wt	Cal/g live wt	Largest deviation from mean (%)	Sulphur in dry material (%)	Live wt equalling 1 g dry wt (g)
Annelida						
Pectinaria hypoborea[a]	0.7	3620	484	1.0	2.1	7.5
Axiothella[a]	2.7	3549	555	0.8	1.1	6.4
Niochamache[b]	0.3	3561	618	–	1.1	5.8
Arthropoda						
Argis dentata, mixed adults	8.0	4544	1203	0.9	0.6	3.8
Hyas araneus	18.3	2610	348	1.0	0.8	7.5
Mollusca						
Yoldia thraciaeformis	19.7	4452	447	0.4	–	10.0
Echinodermata						
Asterias vulgaris	2.7	2014	497	0.8	0.6	4.1
Stongylocentrotus droehbachiensis	8.9	883	287	0.7	0	3.1
Molpadia oolitica	82.0	1684	176	2.2	–	9.6

[a]Based on two determinations.
[b]Based on one determination.

TABLE IV. Caloric content of the standing crop of benthic and epibenthic invertebrates of St. Margaret's Bay, N.S., in kilocalories per square meter.

	Annelida		Arthropoda		Mollusca		Echinodermata		Others		
Station	kcal	%	kcal	%	kcal	%	kcal	%	kcal	%	Total kcal
1	75	95	2	3	1	2	0		0		79
2	17	47	2	5	9	27	0		7	20	35
3	5	19	4	16	14	55	2	9	0		26
4	34	36	5	6	42	45	11	12	1	1	94
5	2	33	2	22	1	9	3	35	0		8
6	5	27	1	7	1	7	12	59	0		19
7	46	38	25	21	21	17	29	24	0		121
8	27	16	17	10	20	11	110	63	0		174
9	62	59	24	22	1	1	20	18	0		107
10	33	56	20	34	1	1	4	6	1	2	59
11	38	50	16	21	19	25	1	2	2	2	77
12	37	57	20	32	2	3	3	4	3	4	64
13	25	41	2	3	1	2	33	54	0		61
14	29	32	2	2	0		58	62	3	3	91
15	23	26	1	2	1	1	64	71	0		89
16	31	34	3	3	1	2	56	61	1		91
17	51	53	4	4	0		41	42	1	1	97
Mean	32	42	9	12	8	11	26	35	1	1	76

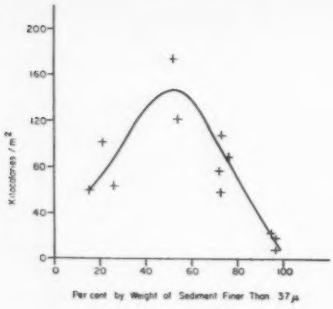

FIG. 2. Calories per square metre present in the standing crop of benthic invertebrates related to sediment size. Curve fitted by eye.

of the food of cod of various sizes from the Gulf of St. Lawrence was given by Powles (1958) as the percent volume occupied by each major phylum in the stomach contents. Using these values with the mean caloric value for each phylum determined here and assuming all food has the same mass per unit volume gives the following average caloric contents of the diet for various-size cod:

Cod size (*cm*):	11–30	31–50	51–70	71–100
% fish in diet	10	25	33	69
Cal/g wet weight	1138	1135	1149	1293

Thus, although the proportion of energy-rich fish in the diet of these cod triples from the first to the third size-groups, the mean caloric content of the food remains constant and only shows a slight rise in the last size-group where fish form 69% of the diet. The extra food energy obtained when a greater fraction of fish is included in the diet is offset by a decrease in crustacea, the richest invertebrate food, and an increase in the lower energy-containing molluscs and echinoderms.

The type of bottom sediment appeared to affect the total calories per square meter present in the standing crop of bottom invertebrates. This was not caused by any of the phyla disappearing from the very sandy or very silty sediments nor was the peak in caloric abundance on muddy sand due to the presence of one species or phylum in great numbers. The echinoderms showed the most erratic changes in their contribution to caloric totals but removing this phylum or its major species *Ctenodiscus* from the total still left a pronounced peak at sediments of equal parts sand and silt. Splitting the totals among infauna and epifauna showed that both groups displayed a similar increase and then decline with increasing silt content. Yonge (1953) describes silt as an unfavourable medium for both infauna and epifauna since locomotion over and through it is difficult and the silt may clog respiratory mechanisms. He notes that pure sand also has disadvantages as it is unstable and burrow walls tend to collapse. There is also the possibility that water speed may

determine both sediment type and the rate of food replacement, the latter regulating the biomass of invertebrates present and their caloric content.

Comparison of the calories present in invertebrates per square meter of bottom of St. Margaret's Bay with values from other areas is difficult as the caloric content of the standing crop elsewhere is not known. As a rough approximation the biomass in gram wet weight per square meter may be multiplied by 644 cal/g, the mean value obtained here. Such conversion gives 27 and 138 kcal/m^2 for muddy sand off the Isle of Man (Jones, 1956) and 29, 17, and 896 kcal/m^2 for the inner continental shelf group of Wigley and McIntyre (1964) taken south of Martha's Vineyard from depths comparable to St. Margaret's Bay. With the exception of this last value all these estimates are within the range shown by the St. Margaret's Bay stations. Lacking information concerning the reproductive and growth rates of species of the St. Margaret's Bay benthic community it is not possible to calculate productivity.

ACKNOWLEDGMENTS

We acknowledge with gratitude the help received from Mr T. Platt who provided salinity data for St. Margaret's Bay and from Drs D. H. Loring and R. W. Sheldon who patiently explained the methods of sediment analysis and the significance of the results. We thank Dr E. Deichman, Museum of Comparative Zoology, Harvard College for identifying *Molpadia oolitica*. The identification of other invertebrates was made easier by comparison with material previously verified by Dr E. L. Bousfield, National Museum of Canada and Dr M. H. Pettibone, Smithsonian Institution. Dr J. A. Allen, Dove Marine Laboratory, Northumberland, kindly sent specimens of *Aphrodite aculeata* for comparison with *A. hastata*.

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La fraye d'une population d'éperlans géants, *Osmerus eperlanus mordax*, au lac Heney, Comté de Gatineau, Québec[1]

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RÉSUMÉ

Deux populations sympatriques d'éperlans *Osmerus eperlanus mordax* cohabitent le lac Heney, Comté de Gatineau, Québec: une population naine et une population géante. C'est cette dernière que nous étudions ici.

Une discussion sommaire sur la théorie des deux populations y est incluse. Les données recueillies à partir de 1556 spécimens récoltés à l'aide de huit filets maillants installés sous la glace d'une localité du lac Heney, en février, mars et avril 1967, ont permis de déterminer la date et le site de la fraye de la population géante; ces deux éléments sont très différents de ceux de la population naine; nous concluons donc que ces deux populations sont reproductivement isolées. Le rapport des sexes au cours de toute la période de fraye est le même que celui des autres populations dulcicoles et marines d'éperlans. Un échantillonneur DeGiusti traîné sur le fond, immédiatement après la débâcle, a permis la récolte d'oeufs embryonnés d'éperlans entre 30 et 40 pieds de profondeur.

L'index de maturité, la fécondité relative et le rapport intergonadal furent spécialement étudiés: le poids des ovaires à maturité représente, en moyenne, le quart du poids total du corps alors que le poids des testicules en est le quarantième; une femelle de 213 mm pond en moyenne 42,460 oeufs; l'ovaire droit est en moyenne 4.5 fois plus petit que le gauche et le testicule droit est en moyenne 3.8 fois plus petit que le gauche.

Il existe une relation directe entre la fécondité totale et la longueur des géniteurs femelles: cette relation s'exprime par la fonction $\log E = 4.54 \log L + k$.

ABSTRACT

Two sympatric smelt populations inhabit Lake Heney, Gatineau County, Quebec. This study deals only with the population which we call "giant" but a brief discussion on "small smelt — large smelt" theory is included. The data were obtained from 1556 specimens collected with eight gillnets set up under the ice at one locality on Lake Heney, in February, March, and April 1967. The data permitted the determination of the time and site of spawning in the giant population. The time and site of spawning in the "dwarf" population was already known, and we found a marked difference in the spawning behavior and time of spawning of the two populations. The two populations are furthermore reproductively isolated. The sex ratio during the spawning period was closely followed and found to be similar to that of all other freshwater or marine smelts. A DeGiusti dredge, dragged along the bottom below the position of the gillnets immediately after the melting of the ice, permitted the collection of embryonic smelt eggs from a depth of 30–40 ft.

The maturity index, relative fecundity, and intergonadal ratio were especially studied. Ovary weight at maturity represents in average one-quarter the total body weight, and testis weight one-fortieth the body weight. A 213-mm female lays an average of 42,460 eggs. The right

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ovary is 4.5 times smaller than the left one, and the right testis is on the average 3.8 times smaller than the left one.

There is a direct relationship between total fecundity and length of mature females. This relation is expressed by the curve $\log E = 4.54 \log L + k$.

INTRODUCTION

On admet généralement que l'éperlan fraye dans un endroit peu profond d'une rivière ou d'un ruisseau à fond rocailleux ou sablonneux balayé par un courant rapide (Creaser, 1926; Kendall, 1927; Langlois, 1935; McKenzie, 1947, 1964; Marcotte et Tremblay, 1948; Rothschild, 1961; Veilleux, MS, 1966; et autres). Cependant, plusieurs auteurs dont Van Oosten (MS, 1940), Lievense (1954), Trautman (1957), Rupp (1959, 1965) et Scott (1967), ont noté plusieurs exceptions où l'éperlan fraye dans la partie la moins profonde (0 à 2 pieds) des plages sablonneuses du lac même. Rupp (1965) précise "Searches by SCUBA divers in water depths down to 15 and 20 feet in 1958 and 1959 revealed that few if any smelt eggs are laid deeper than 18 to 20 inches."

Quant à la date de la fraye, la plupart des auteurs reconnaissent qu'elle se situe quelques jours après le départ des glaces, qu'elle peut varier d'une année à l'autre, et qu'elle est généralement plus tardive dans les régions plus froides. Rupp (1959) mentionne cependant 10 cas dans l'état du Maine où la fraye eut lieu avant le dégel du lac, mais dans des tributaires déjà libres de glace.

Notre étude diffère de celles rapportées ci-dessus en ce que la fraye de la population géante s'effectue un mois avant la débâcle, sous une couverture de 24 pouces de glace, en plus de s'opérer dans le lac même à une profondeur d'au moins 20 pieds d'eau.

Ces travaux, au lac Heney (ou petit lac Poisson Blanc) comté de Gatineau, Québec, ont été effectués au cours des mois de février, mars et avril 1967.

Le lac Heney couvre une superficie de 3075 acres; la profondeur moyenne est de 60 pieds et la profondeur maximum de 115 pieds. Il est situé à 70 milles au nord d'Ottawa dans le bassin de drainage de la rivière Gatineau à 75°54′–75°57′ de long. nord et 45°59′–46°04′ de lat. ouest.

Deux populations sympatriques d'éperlans, *Osmerus eperlanus mordax* (Mitchill) (Fide McAllister, 1963), cohabitent dans le lac: l'une naine, dont les individus atteignent une longueur totale de 3–4 pouces (Delisle, MS, 1965) et l'autre, géante, dont les individus ont 8.5 pouces en moyenne. Elles sont sexuellement isolées par le fait que leurs frayes sont séparées par quelques semaines. Nous n'étudions ici que la population géante.

MATÉRIEL ET MÉTHODES

Au début d'avril 1966, c'est-à-dire avant la débâcle, nous avions capturé des spécimens guais (spent) sous la glace dans la baie Northfield. C'est dans cette partie du lac Heney que nous avons effectué notre travail en 1967. La Fig. 1 indique les cinq points de prélèvement. Les recherches ont été beaucoup

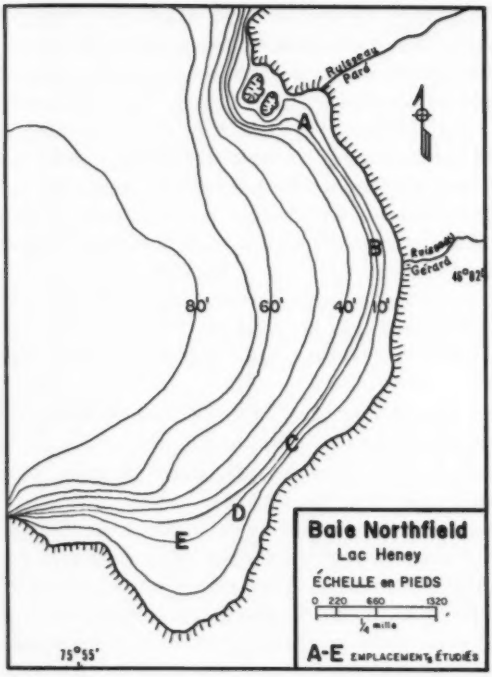

FIG. 1. Représentation bathymétrique de la Baie Northfield du lac Heney situant les cinq localités étudiées.
Bathymetric representation of Northfield Bay of Lake Heney indicating the five localities studied.

plus intenses dans l'emplacement B, parce que c'est là que furent capturés des spécimens guais en 1966. Arbitrairement limité à 9 acres, l'emplacement B (Fig. 2) s'étend du rivage à l'isobathe de 40 pieds et comprend la décharge du ruisseau Gérard. L'accès au ruisseau fut contrôlé par un verveux ouvert vers le lac et ce, à partir du 15 mars, alors que le ruisseau et le lac étaient encore

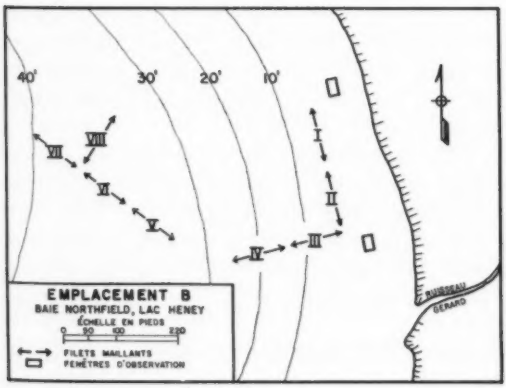

FIG. 2 Emplacement B de la Baie Northfield démontrant les sites des huit filets maillants.
Area B of Northfield Bay indicating the sites of the eight nets.

recouverts de glace. A cet endroit situé au centre de la Baie Northfield, le substratum de glaise est recouvert d'une mince couche de sable et de débris.

Dans l'emplacement B, huit filets maillants de 100′ × 6′ (mailles étirées 1″ et 1½″) ont pêché continuellement du 6 février au 12 avril. Ces filets furent étendus à l'aide d'une trotteuse sous glace (ice jigger) enfilée dans des fenêtres de 3′ × 4′ effectuées au travers de la glace à l'aide d'une vrille mécanique (ice auger). Leur orientation et leur profondeur de pêche sont indiquées sur la Fig. 2. Ils ont été visités 15 fois entre le 2 février et le 17 mars et 19 fois entre le 18 mars et le 12 avril. Des observations ont été faites durant 6 nuits entre le 10 et le 28 mars par deux fenêtres de 3′ × 4′ percées au travers de la glace dans la zone de moins de 10 pieds de profondeur. Après la débâcle, un échantillonneur DeGiusti a été trainé sur le fond de l'emplacement B. Cet instrument est muni d'un treillis métallique assez fin pour retenir des oeufs d'éperlans.

Dans les autres emplacements, c'est-à-dire A, C, D et E, les zones de 10, 20 et 30 pieds furent échantillonnées avec des filets maillants les 24, 25 et 28 mars, dates qui coïncident avec la période où les spécimens capturés dans la localité B augmentaient considérablement en nombre.

Aux mêmes dates, la zone de moins de 10 pieds de profondeur de chacune de ces quatre localités fut l'objet d'observations nocturnes faites à travers des fenêtres dans la glace. La décharge du ruisseau Paré située dans la localité a fut étudiée comme celle du Ruisseau Gérard, décrite précédemment. Il est à noter que ces deux ruisseaux ont un débit très négligeable à cette période de l'année.

Au total, 870 mâles et 686 femelles ont été capturés; ils ont été examinés sur place[4] ou congelés en vue d'une étude ultérieure.

RÉSULTATS

Date et site de la fraye

Désignations des stades de maturité.— Vladykov (1956) reconnait sept stades de maturation des gonades. Nous avons appliqué la nomenclature suivante à notre étude: stade 0: spécimen immature n'ayant encore jamais frayé; stade 1: période de repos ou de latence des gonades, "Quiescent"; stade 2: période d'ébauche de développement; stade 3: période active de maturation; stade 4: période de maturité; stade 5: période de reproduction ou de fraye; stade 6: période post-fraye ou guaie "spent."

Les 261 mâles et les 158 femelles capturés dans la baie Northfield entre le 2 février et le 17 mars étaient tous aux stades de maturité 3 et 4, qui équivalent aux stades III et IV de Nikolsky (1963) (Tableau I).

Les stades de maturité des 609 mâles et des 528 femelles capturés entre le 18 mars et le 12 avril apparaissent au Tableau II. Dans les stades 5–6, ou mi-guai, sont inclus les cas où les gonades étaient déjà partiellement vides

[4]Le département de biologie de l'Université d'Ottawa possède un laboratoire de biologie à cet endroit.

TABLEAU I. Rapport des sexes et stades de maturité des gonades entre le 2 février et le 17 mars 1967.
Sex ratio and stages of maturity of the gonads between February 2 and March 17, 1967.

Mois	Dates	Stade ♂				Stade ♀			
		N	3 et 4	5–6	6	N	3 et 4	5–6	6
			%	%	%		%	%	%
Fév.	2	2	100	–	–	9	100	–	–
	5	6	100	–	–	15	100	–	–
	8	4	100	–	–	15	100	–	–
	14	7	100	–	–	8	100	–	–
	17	1	100	–	–	3	100	–	–
	29	5	100	–	–	5	100	–	–
Total:		25				55			
Pourcentage:		31.0				69.0			
Mars	27	5	100	–	–	4	100	–	–
	3	7	100	–	–	6	100	–	–
	8	16	100	–	–	15	100	–	–
	10	23	100	–	–	14	100	–	–
	11	12	100	–	–	8	100	–	–
	12	25	100	–	–	12	100	–	–
	14	31	100	–	–	15	100	–	–
	15	30	100	–	–	14	100	–	–
	17	87	100	–	–	15	100	–	–
Total:		261				158			

de produits sexuels. Dans cette catégorie se classent 35.3% de tous les mâles et 26.1% de toutes les femelles du Tableau II. Ces forts pourcentages ne s'expliquent pas seulement par le stress et la manipulation des filets; il faut également tenir compte du fait que l'éperlan fraye par étapes successives (Hoover, 1936).

La présence de spécimens mi-guais est un indice particulièrement précieux pour déterminer le *début de la fraye*. Ainsi, parmi les 146 spécimens du 18 mars, 44 mâles et 8 femelles étaient aux stades 5–6. De plus 5 mâles étaient au stade 6. La fraye semble donc avoir débuté avant le 18 mars, c'est-à-dire au moins le 17 mars, même si à cette date nous n'avons pas capturé de spécimens mi-guais dans notre échantillonnage de 102 individus. D'après ces dernières données, il semble plausible que les mâles vident leurs testicules plus rapidement que les femelles expulsent leurs oeufs. Pour déterminer la *fin de la fraye*, il faut plutôt considérer le pourcentage de la population qui a atteint le stade 6. Cet aspect est présenté à la Fig. 3. On y voit que du 18 au 27 mars, le pourcentage des spécimens guais est assez irrégulier. Par la suite, il augmente chez les deux sexes mais plus brusquement chez les mâles. On compte 100% de spécimens guais dans les deux cas le 12 avril. La fraye a pu se prolonger de quelques jours, mais l'état incertain de la glace, ne permit pas de poursuivre les travaux.

TABLEAU II. Rapport des sexes et stades de maturité des gonades entre le 18 mars et le 12 avril 1967.

Sex ratio and stages of maturity of the gonads between March 18 and April 12, 1967.

Mois	Dates	Stade ♂				Stade ♀			
		N	3 et 4	5–6	6	N	3 et 4	5–6	6
			%	%	%		%	%	%
Mars	18	113	56.7	38.9	4.4	33	75.8	24.2	0
	20	93	50.4	46.2	3.4	55	67.3	32.7	0
	22	88	52.3	44.3	3.4	100	80.0	13.0	7.0
	23	31	51.6	48.4	0	29	79.3	20.7	0
	24	20	30.0	65.0	5.0	25	76.0	24.0	0
	25	19	68.4	31.6	0	29	62.1	37.9	0
	27	22	36.4	50.0	13.6	43	62.8	25.6	11.6
	28	25	0	76.0	24.0	33	27.3	57.6	15.1
	29	12	–	–	[a]	21	–	–	[a]
	30	34	26.5	20.6	52.9	35	45.7	31.4	22.9
	31	10	60.0	10.0	30.0	19	52.6	10.5	36.9
Avril	1	20	0	35.0	65.0	26	15.4	46.2	38.4
	3	21	0	0	100.0	7	14.3	42.9	42.8
	5	43	0	18.6	81.4	31	25.8	25.8	48.4
	6	6	0	16.7	83.3	16	0	40.0	60.0
	7	14	14.3	0	85.7	9	11.1	55.6	33.3
	8	13	0	0	100.0	6	0	33.3	66.7
	10	11	0	9.1	90.9	5	0	20.0	80.0
	12	14	0	0	100.0	6	0	0	100.0
Total:		609[b]	217	215	165	528[b]	289	138	80

[a]Les spécimens du 29 mars ne furent pas divisés par stades gonadaux.
[b]Il faut ajouter 21 ♀ et 12 ♂ pour obtenir ces totaux des sommes additionnées.

La fréquence des sexes.— Seulement quelques spécimens épars ont été collectionnés dans les filets des localités A, C, D et E. Dans la localité B, les filets ont été visités 34 fois et 1556 spécimens ont été capturés. Les éperlans mâles représentent 55.9% des captures totales. La répartition des captures d'après les dates et le rapport des sexes apparaissent aux Tableaux I et II. La Fig. 4 reprend ces données en pourcentage du 2 février au 12 avril. On y voit que le pourcentage des mâles atteint son plus haut sommet (85%) le 17 mars, date à laquelle nous établissons le premier jour de la fraye. Dans les jours qui suivent, le pourcentage des mâles diminue jusqu'à être égal à celui des femelles 6 jours après, et atteint son niveau le plus bas (33%) 4 jours plus tard. A partir de ce moment, commence la seconde phase de la fraye: le ré-envahissement de la frayère par les mâles. En 9 jours le pourcentage de ces derniers redevient progressivement égal à celui des femelles, et 6 jours plus tard, c'est-à-dire le 12 avril, il atteint un second sommet de 70% donc 15% inférieur au premier. Ces deux envahissements successifs de la frayère par les mâles constituent un phénomène connu dans les cas où l'éperlan fraye

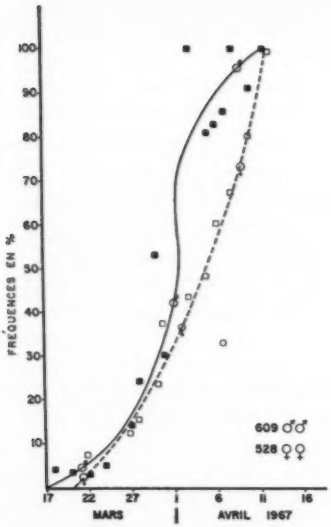

FIG. 3. Pourcentage des mâles et des femelles guais (vides), durant toute la période de fraye.
Percentage of spent (empty) males and females during the entire spawning period.

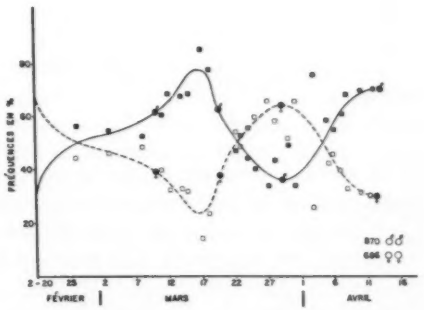

FIG. 4. Variation du pourcentage des sexes mâles et femelles, au cours de la période de fraye de 1967, au Lac Heney.
Variation of the percentage of males and females in the middle of the spawning period of 1967 at Lake Heney.

dans les rivières ou les ruisseaux. Marcotte et Tremblay (1948) le mettent particulièrement en évidence dans leur étude sur quatre saisons de fraye à Grande-Rivière. Ces auteurs sont cependant portés à croire que cette supériorité numérique du sexe mâle est plus factice que réelle. Nous croyons cependant qu'elle est réelle car des filets maillants pêchant constamment représentent plus fidèlement les mouvements d'une population qu'un échantillonnage fait à l'épuisette. Afin de démontrer la similitude dans l'allure des courbes entre une population géante dulcicole et une population d'eau salée, les résultats de la saison de fraye pour l'année 1945, de Marcotte et Tremblay (1948), sont présentés à la Fig. 5. Cette représentation graphique de la variation du pourcentage des sexes, au cours de la période de fraye dans un ruisseau, est différente de la nôtre (Fig. 4) en un point. Elle ne possède pas la partie équivalente entre le 2 février et le 17 mars de notre courbe. Cette partie nous fait voir, du 2 février au 8 mars, un échantillonnage normal de la population du lac et par la suite, jusqu'au 17 mars, un envahissement progressif de la frayère par les géniteurs mâles. Le graphique de Marcotte et Tremblay ne représente pas la migration reproductrice ou migration de fraye décrite par Magnin et Beaulieu (1965) puisque les spécimens étaient capturés une fois parvenus à la frayère.

Récolte d'oeufs sur les frayères.— Cent vingt-sept oeufs embryonnés d'éperlans furent récoltés sur le fond, avec un échantillonneur DeGiusti, entre 30

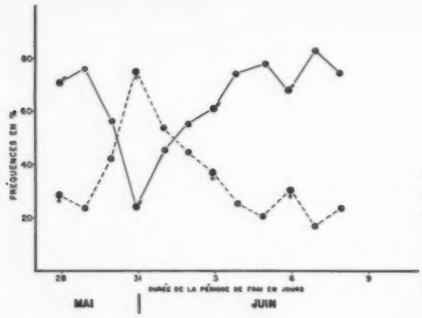

FIG. 5. Variation du pourcentage des mâles et des femelles, au cours de la période de fraye de 1945, Grande-Rivière, Gaspé, Québec. (D'après Marcotte et Tremblay, 1948).
Variation of the percentage of males and females in the middle of the spawning period of 1945, Grande-Riviere, Gaspé, Québec. (From Marcotte and Tremblay, 1948.)

et 40 pieds de profondeur, les 25 et 27 avril, c'est-à-dire 2 et 4 jours seulement après la débâcle. L'âge de ces oeufs variait de 12–18 jours (Clulow, MS, 1964). Ceci indique qu'ils ont été fécondés à la fin de la période de fraye.

Prédation des oeufs d'éperlans.— L'examen de 134 oeufs prélevés dans l'estomac d'un éperlan mâle capturé le 27 mars révéla qu'il s'agissait d'oeufs pédicellés d'éperlans. Ces oeufs étaient embryonnés mais leur état de digestion ne permettait pas d'en déterminer l'âge exact. Il s'agissait cependant d'oeufs au stade post-gastrulaire. Il y eut également prédation des oeufs d'éperlans par des perchaudes *Perca flavescens* qui envahirent la frayère dans les premières semaines d'avril.

Site de la frayère et théorie des deux populations.— Aucun éperlan géant n'a été capturé, dans les verveux, à l'entrée des deux ruisseaux Gérard et Paré. Aucun rassemblement d'adultes, caractéristique de la fraye de l'éperlan, n'a été observé à travers la glace par les fenêtres d'observation s'ouvrant sur le fond de la zone de moins de 10 pieds de profondeur. Les filets I, II, III et IV (Fig. 2) étendus dans moins de 20 pieds d'eau donnèrent une moyenne de capture de 4 éperlans par filet par 24 hr de pêche. Les filets étendus entre les isobathes de 20 à 40 pieds donnèrent une moyenne de 18 éperlans. Il semble donc que la frayère se situe en profondeur plutôt que le long des rivages comme c'est le cas pour la population naine du même lac, après la débâcle, vers la fin du mois d'avril. Le fait que des oeufs embryonnés d'éperlans aient été récoltés dans plus de 20 pieds d'eau et que la Fig. 4, caractéristique à toute fraye d'éperlans, ait été tracée à partir de spécimens capturés dans les filets V, VI, VII et VIII confirme cette déduction. Les géniteurs n'étaient donc pas en route vers la frayère mais frayaient vraisemblablement à cet endroit.

Il est à noter qu'entre le 15 mars et le 5 avril, c'est-à-dire, pendant la période active de la migration reproductrice, nos filets maillants n'ont capturé que des éperlans. Ces derniers ayant envahi le terrain de fraye nous ne capturions plus les autres espèces de poissons qui représentaient toujours un fort pourcentage de notre échantillonnage avant le 15 mars et après le 5 avril. Ces autres espèces de poissons sont par ordre d'importance: *Perca flavescens, Esox lucius, Percopsis omiscomaycus, Coregonus artedii, Cristivomer namaycush,*

Coregonus clupeaformis, Catostomus commersoni, Ictalurus punctatus, Ameiurus nebolosus, Cottus ricei et *Myoxocephalus thompsonii.*

Brooks and Deevey (1963) cite: "Never have any conspicuous differences in the spawning sites selected by the two forms been noted." Quant on sait que la population naine du lac Heney fraye à la fin d'avril sur les plages de sable et de gravier on peut assumer qu'il y a une différence notoire de frayère entre ces deux populations sympatriques.

Reuter (1883) cité dans Kendall (1927) mentionne: " 'La grosse variété' d'éperlans *Osmerus eperlanus eperlanus* des lacs de la Finlande choisit des eaux rapides et *profondes* pour frayer, tandis que la 'petite variété' au contraire fraye sur les talus ou les plages peu profondes des lacs." Cette assertion correspond à la situation au lac Heney sauf qu'il n'est pas question d'eau rapide. Il y a d'autre part inversion dans le temps de la fraye: Reuter note en effet que la "petite variété" fraye avant la "grosse."

Les résultats partiels que nous reportons en faveur de la théorie des deux "populations," "races," ou "variétés," selon les auteurs, sont donc en dissension avec Rupp (1966). Cette théorie est soutenue par Kendal (1913, 1927), Greene (1930), Zilliox and Youngs (1958) et Brooks and Deevey (1963). Rupp (1966) démontre que le taux de croissance de l'éperlan peut changer remarquablement quand le poisson est transféré dans un nouvel environnement. Il cite également: "The supposed existence of two "kinds" of smelts, "small smelts" and "large smelts", some living allopatrically and others living sympatrically, depends ultimately upon the assumption that smelt growth rates are controlled by genotypic factors which have sufficient penetrance to negate or virtually negate any environmental effects." Nous sommes d'accord avec sa démonstration et sa citation. Mais, il faut considérer que Rupp n'a pas expérimenté avec des populations sympatriques ayant évolué dans un même environnement. Seules des populations allopatriques géantes et naines firent l'objet de ses recherches. Nous sommes convaincus et nous avons observé dans différents autres lacs que des populations allopatriques peuvent subir d'importantes variations dans leur écologie et leur éthologie. De telles variations impliquant des différences dans leur constitution génétique, c'est-à-dire une spéciation allopatrique (Mayr, 1963; Svärdson, 1961). Mais quand deux populations indigènes ont évolué sympatriquement, et qu'il y a impossibilité temporelle de croisement (interbreeding) entre les deux populations, on peut alors croire qu'il s'agit là de deux populations distinctes et que leur croissance, est contrôlée génétiquement.

Une étude détaillée sur l'âge, les relations longueur–poids et autres aspects de la biologie comparative des deux populations du lac Heney fera l'objet d'un travail subséquent.

Index de maturité.— Afin d'établir le degré de maturité, le poids des deux gonades fut converti en pourcentage du poids total du corps des géniteurs. C'est l'"index de maturité" que Magnin (1962) et Cuerrier (1966) appellent "rapport gonosomatique." Plus l'index est élevé, plus grand est le degré de maturité (Fig. 6). La formule utilisée est: $\frac{G \times 100}{P}$ où G exprime

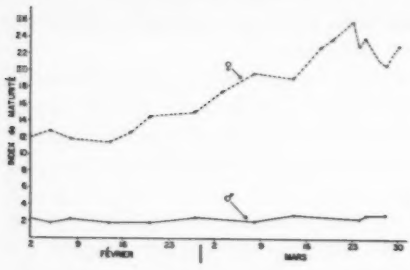

FIG. 6. Index de maturité des gonades mâles et femelles du 2 février au 30 mars 1967.
Index of maturity of the male and female gonads from February 2 to March 30, 1967.

le poids des gonades (ovaires ou testicules), et P, le poids total du poisson. Cet index nous permet de mieux analyser l'évolution dans le développement des gonades, en suivant leurs changements de poids, selon leur maturation; il a déjà été utilisé entre autres par Vladykov (1951) dans le cas de la lamproie.

Cent soixante-cinq femelles et 70 mâles furent utilisés dans cette étude de maturation (Tableaux III et IV). A cette fin, nous avons éliminé les géniteurs à demi-guais (stades 5–6) et tous les spécimens ayant perdu des gamètes

TABLEAU III. Évolution dans le degré de maturité des ovaires de 165 femelles.
Changes in the degree of maturity of ovaries of 165 females.

Mois	Dates	N	Éperlan géant		Poids moy. des ovaires (*g G*)	Index de maturité $\frac{G \times 100}{P}$
			Long. moy. (*mm*)	Poids moy. (*g P*)		
Fév.	2	9	210	62.83	7.52	11.95
	5	15	205	59.98	7.54	12.78
	8	15	203	59.11	7.03	11.91
	14	8	189	49.77	5.76	11.57
	17	3	174	37.70	4.72	12.52
	20	5	197	56.02	8.18	14.58
	27	4	197	56.00	8.45	15.09
Mars	3	6	200	57.20	9.99	17.47
	8	10	209	60.77	12.01	19.76
	14	10	210	65.98	12.62	19.13
	18	10	213	69.12	15.74	22.77
	20	10	220	75.03	17.87	23.82
	23	10	207	60.84	15.80	25.97
	24	5	184	40.24	9.25	22.99
	25	5	213	71.03	17.01	23.95
	27	5	180	43.29	9.26	21.39
	28	10	219	73.01	15.16	20.76
	29	10	211	61.54	13.62	22.13
	30	15	208	60.45	14.01	23.18
Total:		165				
Moyenne:			203	58.94	11.13	18.88

TABLEAU IV. Évolution dans le degré de maturité des testicules de 70 mâles.
Changes in the degree of maturity of testicules of 70 males.

Mois	Dates	N	Éperlan géant		Poids moy. des testicules (*g G*)	Index de maturité $\frac{G \times 100}{P}$
			Long. moy. (*mm*)	Poids moy. (*g P*)		
Fév.	2	2	196	46.64	.98	2.10
	5	5	198	53.93	.98	1.82
	8	4	191	46.95	1.01	2.15
	14	7	186	43.50	.84	1.93
	20	5	190	42.85	.82	1.91
	27	4	189	45.28	1.09	2.41
Mars	8	5	194	44.70	.91	2.04
	14	10	189	42.86	1.22	2.85
	24	15	185	37.27	.90	2.41
	25	3	187	38.46	1.08	2.81
	28	10	188	41.11	1.20	2.92
Total:		70				
Moyenne:			190	43.96	1.00	2.27

soit dans les filets soit par manipulation. Nous avons donc basé nos calculs sur les 235 spécimens qui restaient. Les gonades furent toujours pesées à l'état frais sur une balance précise au centième de gramme. Entre le 2 février et le 30 mars, l'index de maturité pour les femelles varie entre 11.57 et 25.97 et entre 1.82 et 2.92 pour les mâles. Le poids des ovaires à maturité représente donc grossièrement le quart du poids total du corps comme on le remarque dans l'échantillonnage du 23 mars (Tableau III). Les données de Masterman (1913) sur *Osmerus e. eperlanus* de l'Angleterre ressemblent étrangement aux nôtres sur ce dernier aspect ainsi qu'à d'autres points de vue. Il est à remarquer que l'index de maturité est relativement stable jusqu'au 17 février et que pendant les semaines qui suivent les ovaires doublent leur poids (Fig. 6).

Quant aux mâles (Tableau IV), l'évolution dans le degré de maturité est moins important que pour le cas des femelles. Le poids des testicules à maturité ne représente qu'approximativement le quarantième du poids total du corps. La pesée des gonades mâles et femelles s'est terminée à la fin du mois de mars; les géniteurs n'ayant pas perdu de gamètes se faisaient alors de plus en plus rares et il était alors impossible de déterminer si des produits sexuels n'avaient pas été évacués.

DONNÉES GÉNÉRALES

Fécondité relative et totale.— Pour évaluer la fécondité, nous avons calculé le nombre d'oeufs contenus dans 500 mg d'ovaire et estimé à partir de là le nombre total d'oeufs contenus dans l'ovaire dont le poids était connu. Ce résultat nous donne la fécondité relative (Vladykov, 1951, 1956). Par

fécondité totale on entend le nombre total d'oeufs (ovules murs) présents dans les deux ovaires. Les oeufs d'éperlans étant très petits, et le poids du tissu ovarien chez la femelle à maturité très négligeable en proportion du poids total des oeufs, nous avons préféré cette méthode à la méthode volumétrique (Vladykov et Legendre, 1940). Le dénombrement des oeufs par 500 mg d'ovaire fut toujours fait par la même personne afin de minimiser le taux d'erreurs. Après la pesée, ces oeufs frais furent fixés dans la formaline à 5% pour faciliter leur comptage.

On sait que le nombre d'oeufs compris dans un certain poids d'ovaire, dépend de leur diamètre. Seules les trente femelles mûres (stades 4 et 5) capturées les 18, 20 et 23 mars (Tableau III) furent utilisées. Les résultats obtenus (Tableau V) visent donc à présenter le nombre approximatif d'oeufs pondus durant la fraye de la population géante d'éperlans. Ce nombre atteint 42,460 oeufs en moyenne, pour des spécimens de 213 mm de longueur totale moyenne.

Il est connu qu'il y a une relation directe entre la fécondité totale et la longueur du poisson. Ricker (1932), Vladykov (1956), Smith (1947) et autres, ont établi que cette relation était de type curvilinéaire. La Fig. 7 illustre ce phénomène sur échelle logarithmique à partir de 10 des 31 femelles du Tableau V et de 7 autres femelles de plus petites dimensions apparaissant au Tableau VI et faisant partie d'autres échantillonnages. Contrairement à Bailey (1964) qui avait un échantillonnage, trois fois plus petit que le nôtre, nous obtenons une relation positive entre la longueur du poisson et le nombre total d'oeufs produits. McKenzie (1964) utilisant la même méthode à partir d'observations provenant de neuf spécimens seulement, obtient une pente de 4.4 ce qui est très rapproché de notre résultat de 4.54.

Diamètre des oeufs ovariens.— Après une mesure linéaire de 20 oeufs ovariens chez tous les spécimens utilisés à cette étude, le diamètre des oeufs était sensiblement le même variant entre .85 et .95 mm.

Rapport intergonadal.— Chez la plupart des espèces de poissons, les deux gonades ont à peu près le même poids et le même volume. Chez l'éperlan, la gonade droite est beaucoup plus petite que la gonade gauche. Le rapport entre le poids des gonades chez l'éperlan a été peu étudié et aucun auteur ne donne la valeur mathématique de ce rapport; c'est pourquoi nous avons cru bon d'inclure cet aspect du problème. Le rapport intergonadal s'exprime par $\frac{\text{G.D.} \times 100}{\text{G.G.}}$ où G.D. exprime le poids de la gonade droite (ovaire, ou testicule), et G.G., le poids de la gonade gauche. La pesée individuelle des deux gonades fraîches pour chacun des deux sexes a été effectuée jusqu'au 3 mars. Après cette date, les deux gonades, surtout les ovaires, étaient trop difficiles à séparer l'une de l'autre, étant donné leur maturité. D'après nos données, on voit que l'ovaire droit représente, en moyenne, 22% du poids de l'ovaire gauche et que le testicule droit représente, en moyenne, 26% du poids du testicule gauche (Tableau VII).

Il semble toutefois, chez les femelles, que plus la période active de maturation est avancée, plus le rapport ovaire droit sur ovaire gauche, diminue.

TABLEAU V. Nombre d'oeufs présents dans 30 femelles à maturité (stade 4 et 5) des 18, 20 et 23 mars 1967.
Number of eggs present in 30 females at maturity (stage 4 and 5) on March 18, 20, 23, 1967.

Dates	No.	Éperlan		Ovaires			Index de maturité $\frac{G \times 100}{P}$
		Longueur (*mm*)	Poids (*g P*)	Poids (*g G*)	No. d'oeufs dans 500 mg	No. d'oeufs total	
18 Mars	1	235	79.06	20.79	1,198	49,813	26.30
	2	204	55.07	12.84	1,300	33,384	23.32
	3	209	74.07	18.28	1,360	49,722	24.68
	4	237	86.51	21.97	1,274	55,980	25.40
	5	203	63.97	12.79	1,454	37,193	19.99
	6	210	76.16	19.89	1,099	43,718	26.12
	7	196	54.31	10.51	1,406	29,554	19.35
	8	198	56.42	10.96	1,501	32,902	19.43
	9	220	74.13	15.79	1,398	44,149	21.30
	10	213	71.49	13.61	1,470	40,013	19.04
20 Mars	11	249	94.79	19.34	1,396	53,997	20.40
	12	208	59.29	15.84	1,234	39,093	26,72
	13	250	104.65	25.15	1,364	68,609	24.03
	14	207	57.89	15.79	1,305	41,212	27.28
	15	214	73.50	16.19	1,290	41,770	22.03
	17	205	57.18	12.99	1,347	34,995	22.72
	16	210	76.98	18.61	1,266	47,121	24.18
	18	250	96.18	23.76	1,200	57,024	24.70
	19	209	73.48	18.87	1,270	47,930	25.68
	20	196	56.32	12.13	1,540	37,360	21.54
23 Mars	21	211	54.89	14.66	1,149	33,689	26.71
	22	181	41.05	11.60	1,202	27,886	28.26
	23	204	59.12	14.13	1,303	36,823	23.90
	24	208	63.50	17.61	1,260	44,377	27.73
	25	212	55.19	14.72	1,145	33,709	26.67
	26	180	39.98	11.16	1,112	24,820	27.91
	27	203	57.98	13.92	1,289	35,886	24.01
	28	209	65.12	17.91	1,275	45,671	27.50
	29	249	101.60	24.98	1,102	55,056	24.59
	30	209	70.01	17.32	1,160	40,182	24.74
Moyenne:		213	68.33	16.47	1,289	42,460	24.10
5 Fév.*		290	176.80	25.36	1,570	79,630	14.34

*Il s'agit du plus gros spécimen capturé dans nos filets maillants.

Il est donc plausible que le plus gros ovaire en se développant et en remplissant la plus grande partie de la cavité abdominale, le fasse au détriment de l'ovaire droit, réduisant ainsi sa productivité d'oeufs (Svärdson, 1949). Il y aurait avantage à approfondir ce dernier point peu exploité dans cette étude.

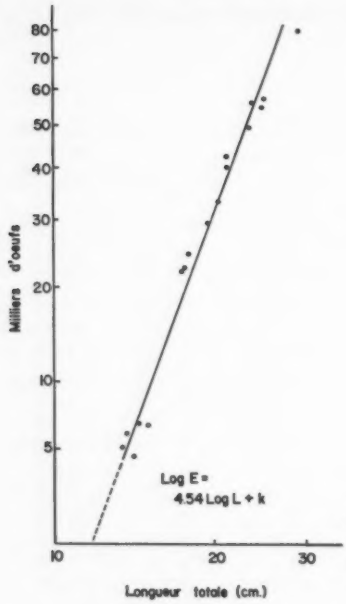

FIG. 7. Fécondité totale des éperlans géants du lac Heney en relation avec la longueur totale.
Total fecundity of the giant smelt of Lake Heney in relation to their total length.

TABLEAU VI. Nombre d'oeufs présents dans sept femelles de longueur minimum et capturées dans les échantillonnages de février et mars 1967.
Number of eggs present in seven females of minimum length captured in the February and March 1967 samples.

		Éperlan		Ovaires			
Dates	No.	Longueur (*mm*)	Poids (g)	Poids (g)	No. d'oeufs dans 500 g	No. d'oeufs total	Index de maturité
14 Fév.	1	144	17.92	2.20	1,560	6,864	12.28
	2	150	18.60	2.25	1,509	6,791	12.10
20	3	142	16.15	1.31	1,731	4,538	8.11
24 Mars	4	137	13.10	2.32	1,289[a]	5,981	17.71
27	5	135	13.75	1.98	1,289[a]	5,104	14.40
	6	176	41.02	8.71	1,289[a]	22,454	21.23
30	7	175	40.76	8.64	1,289[a]	22,274	21.20

[a]Nombre se référant à la moyenne du Tableau V.

DISCUSSION

D'après nos données, la durée de la fraye de l'éperlan géant au lac Heney serait de 27 jours, soit 12 jours de plus que la moyenne des cas rapportés dans la littérature. D'après la littérature il semble que plus la température est

TABLEAU VII. Rapports intergonadaux chez l'éperlan géant du lac Heney, au cours de la période de maturation (stade 3).
Intergonadal ratio on Lake Heney giant smelt during the maturation period (stage 3).

		Femelles				Mâles			
Mois	Dates	N	Poids moy. ovaires g. (g)	Poids moy. ovaires dr. (g)	Rapport	N	Poids moy. testicules g. (g)	Poids moy. testicules dr. (g)	Rapport
Fév.	2	10	6.06	1.46	24.09	2	.73	.25	34.25
	5	15	5.95	1.57	26.39	5	.77	.21	27.27
	8	15	5.69	1.34	23.55	4	.83	.18	21.69
	14	8	4.72	1.04	22.03	7	.77	.17	22.08
	17	3	3.99	.73	18.30	–	–	–	–
	20	5	6.85	1.33	19.42	5	.65	.17	26.15
	27	4	7.00	1.45	20.71	4	.86	.23	26.74
Mars	3	6	8.30	1.69	20.36	–	–	–	–
Total:		66				27			
Moyenne:			6.07	1.33	21.91		.77	.20	25.97

basse, plus la fraye se prolonge. C'est d'ailleurs ce qu'avaient remarqué Marcotte et Tremblay (1948). On admet généralement que la température moyenne de l'eau au moment de la fraye est près de 7 C. Dans le cas étudié ici, la température n'a jamais atteint plus de 4 C. Ce fait explique que la fraye sous la glace soit d'une durée plus longue que celle qui a lieu après le départ des glaces.

Au sujet du site de la frayère, les données disponibles permettent de conclure qu'en 1967, l'éperlan géant n'a pas frayé dans les deux ruisseaux de la baie Northfield. Cependant, nos données sont trop incomplètes pour tirer des conclusions aussi catégoriques quant à la fraye en dehors de notre région d'expérimentation (localité B). Même si les preuves en faveur de la fraye entre les isobathes de 20–40 pieds de l'emplacement B ne sont pas à l'abri de toute objection, elles semblent néanmoins assez fondées. Le fait qu'il ne faut pas négliger les profondeurs quand on étudie des problèmes de ce genre, nous est d'ailleurs communiqué par le Dr R. G. Ferguson (résultats non publiés) qui collectionna, à différents endroits du lac Erié, à l'aide de l'échantillonneur DeGiusti, des oeufs d'éperlans sur différents substrata. En effet, en 1964, à l'est de Point Pelee, il collectionna plus de mille oeufs d'éperlans à 54 pieds de profondeur et à plus de 10 milles du rivage. Egalement à Long Point Bay, au sud de Port Dover, il collectionna des oeufs jusqu'à 100 pieds de profondeur, mais en moyenne entre 25 et 50 pieds. Son étude, Ferguson (1965), démontra que l'éperlan s'adapte facilement à differentes profondeurs.

Green (1930) entrevoit également cette possibilité de fraye en profondeur en citant: "It is the author's belief that one of the main spawning grounds of Lake Champlain smelts, is to be found in the lake near Port Henry, possibly in water ten feet deep or more."

L'index de maturité est également un outil important en vue de déterminer le moment où les gonades atteignent leur développement maximum. C'est le 23 mars, qu'on trouve l'index de maturité le plus élevé. C'est également à cette date que la fraye atteint son intensité maximum alors que mâles et femelles sont, pour une première fois, en nombres égaux (Fig. 4). Ce dernier point apporte également une preuve en faveur de l'hypothèse qu'un nombre critique de géniteurs femelles est nécessaire pour le stimulus déclanchant la ponte et la fécondation.

En ce qui concerne la fécondité totale, les nombres d'oeufs que nous avons estimés chez l'éperlan géant du Lac Heney, correspondent assez bien avec les résultats de Bailey (1964). Cependant McKenzie (1964) estime à 69,600 le nombre d'oeufs contenus dans une femelle de 20.9 cm (8.3 pouces) et à 8500 le nombre d'oeufs dans une femelle de 12.7 cm. Ces résultats nous semblent surestimés d'autant plus que cet auteur ne donne pas la méthode utilisée. Contrairement à McKenzie (1964), Baldwin (1950) estime à 22,600 le nombre d'oeufs chez une femelle de 8.8 pouces. Cet estimé est certainement inférieur à la réalité et il s'agissait sans doute d'une femelle ayant expulsé certains de ses oeufs. La méthode utilisée pour cette estimation n'est pas indiquée. Les ovaires des numéros 1–5 inclusivement du Tableau VI semblent contenir peu d'oeufs, mais Kendall (1927), par un dénombrement direct, trouva 5893 oeufs dans les ovaires d'une femelle de $4\frac{5}{8}$ pouces (117 mm) ce qui demeure dans l'ordre de grandeur de nos résultats. Aucun travail connu des auteurs se rapporte aux rapports inter-gonadaux. Ces résultats ne portent donc pas à comparaison.

CONCLUSIONS

1. En se basant: (*a*) sur l'allure des courbes de fréquence des sexes en fonction du temps, entre le 17 mars et le 12 avril; (*b*) sur la période que met la population pour atteindre le stade 6 de maturité; (*c*) sur la détermination de l'âge des oeuf embryonnés collectionnés; (*d*) sur l'index de maturité, il semble qu'au lac Heney la fraye a commencé 37 jours avant le départ des glaces a duré 27 jours et s'est terminée 10 jours avant la débâcle.

2. La température de 4 C sur le fond de l'emplacement B et particulièrement entre les isobathes de 20–40 pieds, prolonge la période de fraye.

3. En se basant sur l'abondance relative des captures et sur la provenance des oeufs embryonnés, la frayère semble située entre les isobathes de 20–40 pieds.

4. La population naine du lac Heney fraye après la débâcle, i.e. généralement pas avant la fin d'avril, le long des rivages du lac, et non dans les deux principaux tributaires mentionnés. A l'aide de cette mise au point et des conclusions précédentes nous pouvons établir que le comportement de fraye de ces deux populations est différent, et qu'en plus elles sont sexuellement isolées.

5. Au cours de la période de fraye, l'allure des courbes de fréquence des sexes en fonction du temps (Fig. 4) semble la même pour toutes les populations dulcicoles et marines d'éperlans.

6. Le poids des ovaires à maturité représente grossièrement le quart du poids total du corps et le poids des testicules, le quarantième.

7. L'ovaire droit est en moyenne 4.5 fois plus petit que le gauche, tandis que le testicule droit est en moyenne 3.8 fois plus petit que le gauche.

8. Il existe une relation directe entre la fécondité totale et la longueur des éperlans femelles.

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Âge et croissance du Maskinongé, *Esox masquinongy*, dans quatre lacs du Québec[1,2]

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RÉSUMÉ

Les spécimens provenaient de quatre lacs: deux où le Maskinongé est indigène, le lac Saint-François (188 spécimens) et le lac Saint-Louis (109 spécimens) et deux où il fut introduit, le lac Saint-Joseph (44 spécimens) et le lac Ouareau (12 spécimens). La détermination de l'âge des Maskinongés fut faite à l'aide des écailles. La croissance en longueur et en poids est identique chez les mâles et les femelles et elle est identique chez les Maskinongés des lacs Saint-François et Saint-Louis. La croissance est par contre très différente dans les lacs Saint-Joseph et Ouareau: au cours du 11ième été de leur vie, par exemple, les Maskinongés des lacs Saint-François et Saint-Louis mesurent 1112 mm, et pèsent 10,511 g tandis que ceux du lac Saint-Joseph mesurent 1024 mm et pèsent 8854 g et ceux du lac Ouareau mesurent 914 mm et pèsent 5669 g. Nous avons comparé nos résultats avec ceux de la littérature.

ABSTRACT

Specimens were taken from two lakes where maskinonge is indigenous: Lake Saint-François (188 specimens) and Lake Saint-Louis (109 specimens), and from two others where it was introduced: Lake Saint-Joseph (44 specimens) and Lake Ouareau (12 specimens). The ages were determined from scales reading. Growth in length and in weight was identical for males and females from lakes Saint-François and Saint-Louis and there was no difference in growth observed in these same two lakes. Growth, however, was very different in lakes Saint-Joseph and Ouareau: during their 11th summer for instance, maskinonges from lakes Saint-François and Saint-Louis measured 1112 mm, and weighed 10,511 g whereas those from Lake Saint-Joseph measured 1024 mm and weighed 8854 g and those from Lake Ouareau measured 914 mm and weighed 5669 g. Our results are compared with those in the literature.

INTRODUCTION

PEU DE TRAVAUX ont été faits sur la croissance des Maskinongés (*Esox masquinongy* (Mitchill)). Au Canada, on ne peut guère citer que les travaux de Hourston (MS, 1949 et 1952), Crossman (1956) et Muir (1960) en Ontario et celui de Couture (1964) au Québec. Aux Etats-Unis nous citerons les travaux de Moore (1926) dans l'Etat de New-York de Schloemer (1936) et Juday et Schloemer (1938) au Wisconsin et de Buss et Miller (1961) en Pennsylvanie.

Un abondant matériel, récolté par l'Office de Biologie du Ministère de la Chasse et des Pêcheries du Québec, a été mis à notre disposition et nous a permis de faire ce travail sur ce poisson intéressant tant au point de vue

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biologique qu'au point de vue pêche sportive. Après avoir décrit le matériel et les méthodes utilisées, nous donnerons nos résultats et nous confronterons enfin nos données avec celles de la littérature.

MATÉRIEL ET MÉTHODES

Les Maskinongés provenaient des lacs suivants (Fig. 1): le lac Saint-François, un élargissement du fleuve Saint-Laurent qui reçoit les eaux des Grands-Lacs; le lac Saint-Louis qui lui fait suite et dans lequel se jette une partie des eaux provenant de l'Outaouais; le lac Saint-Joseph qui se déverse dans le Saint-Laurent par la rivière Bécancour, en aval de Trois-Rivières; le lac Ouareau dont les eaux s'écoulent aussi dans le Saint-Laurent par la rivière Ouareau et par la rivière L'Assomption. Dans les lacs Saint-Francois et Saint-Louis, il s'agit d'une population naturelle de Maskinongés. Les lacs Saint-Joseph et Ouareau reçurent respectivement 500 fretins le 11 août 1951 et 2000 fretins le 26 juillet de la même année. Aucun ensemencement subséquent n'eut lieu avant le moment où s'effectuèrent les captures, soit en 1959, 1960 et 1961.

La longueur exprimée en millimètres fut mesurée en plaçant la nageoire caudale en position naturelle; il ne s'agit donc pas de la plus grande longueur possible du poisson, que Lagler (1949) et Legendre (1954) conseillent d'utiliser. Le poids fut mesuré en grammes. Le sexe fut déterminé par un examen macroscopique des gonades.

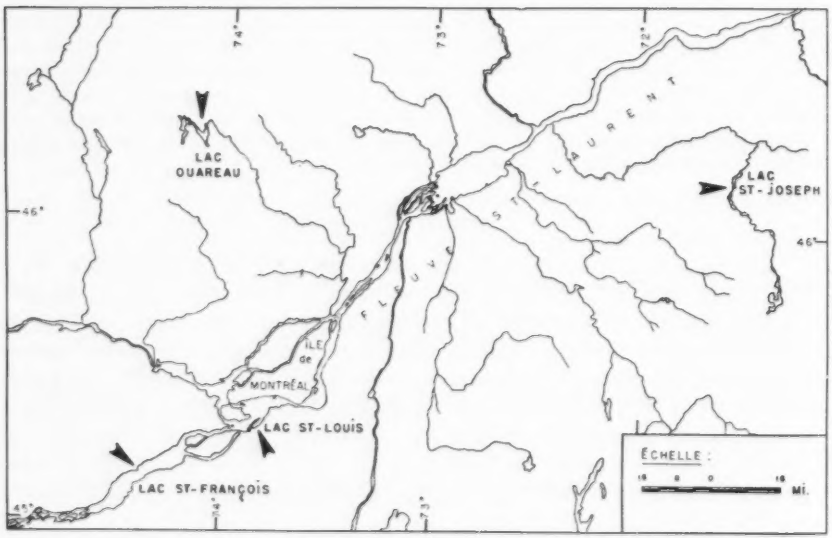

FIG. 1. Endroits de prélèvement des Maskinongés.
Sampling areas for maskinonge.

Johnson (1960) a démontré que l'âge des Maskinongés peut être déterminé avec autant de certitude à partir des écailles qu'à partir des vertèbres ou des coupes transversales de la ceinture pelvienne. Nous avons utilisé les écailles. Les annuli étaient observés à la loupe binoculaire et dessinés à la chambre claire (grossissement = 14). La lecture des zones de croissance saisonnière sur les écailles est souvent assez ardue (Fig. 2). Le premier annulus en particulier est souvent difficile à trouver; afin de mieux le préciser, nous avons examiné les écailles de 203 spécimens d'âge connu, élevés en pisciculture et dont l'âge variait de 6 mois à 4 ans. Nous avons désigné par le chiffre 0 le groupe d'âge d'un poisson qui se trouve dans l'année de son éclosion, par I, II...le poisson qui a passé 1, 2...hivers. Le groupe d'âge est ainsi synonyme du nombre d'hivers révolus ou encore du nombre d'annuli sur l'écaille.

A partir des données obtenues par la lecture des écailles, nous avons d'abord calculé, pour chaque groupe d'âge, la moyenne des longueurs et des poids des spécimens qui la composent ainsi que l'écart type sur les valeurs individuelles. Nous avons aussi cherché la relation qui pouvait exister entre la longueur totale du Maskinongé (Y), et la distance entre le foyer de l'écaille et les différents annuli (X), distance mesurée sur le dessin de l'écaille grossie 14 fois. En utilisant le millimètre comme unité, l'équation de régression établie à partir de 68 spécimens du lac Saint-Louis est de la forme:

$$Y = 27.200 + 11.109\ X.$$

Le coefficient de corrélation est égal à 0.89. L'ordonnée à l'origine est 27.200 mm; cette valeur, n'est cependant pas différente de zéro au point de vue statistique. En effet, à un niveau de probabilité de 1%, le test de F sur l'homogénéité des variances donne 2.48, valeur très inférieure à celle de la table (7.04). Nous n'avons donc pas tenu compte de cette constante dans nos rétrocalculs des longueurs des poissons à partir du rayon des annuli.

Nous avons tenté d'exprimer mathématiquement les croissances en longueur et en poids des Masquinongés en fonction de l'âge. Nous avons calculé les équations de régression exprimant le logarithme de la longueur ou du poids en fonction du logarithme de l'âge. Ces équations linéaires se prêtent facilement à une analyse statistique. On a pu étudier ainsi s'il y avait des différences de croissance suivant les sexes et suivant les différents milieux.

RÉSULTATS

Comparaison des croissances en longueur et en poids des Maskinongés suivant le sexe et le milieu

Le Tableau I donne les différentes équations de régression du logarithme de la longueur (log L) ou du logarithme du poids (log P) en fonction du logarithme de l'âge (log A) de plusieurs catégories de poissons. La comparaison statistique de ces droites permet de tirer les conclusions suivantes à un niveau de probabilité d'erreur de 1%.

TABLEAU I. Comparaison des différences de pente et de position des équations de régression exprimant le logarithme de la longueur totale en millimètres (log L) et du logarithme du poids en grammes (log P) en fonction du logarithme de l'âge (log A) entre les Maskinongés de sexes différents et entre les Maskinongés de différents milieux. *f* = femelles, *m* = mâles, *i* = indéterminés, N = effectif, *r* = coefficient de corrélation, F_c = F calculé, F_t = F tabulé, * = probabilité qu'il n'existe pas de différences à un niveau de probabilité d'erreur de 1 %.

*Comparison of the differences of slope and the position of the regression equations expressing the logarithm of the total length in millimeters (log L) and the logarithm of weight in grams (log P) in the function of the logarithm of age (log A) between the maskinonge of different sexes and of different environments. f = females, m = males, i = undetermined, N = effective, r = coefficient of correlation, F_c = F calculated, F_t = F tabulated, * = significant difference is 1%.*

Échantillons comparés	Equations	N	*r*	Différences de pente		Différences de position	
				F_c	F_t	F_c	F_t
Lac St-François, *f*	log L = 2.618 + 0.432 log A	64	0.85				
" " *m*	log L = 2.620 + 0.434 log A	50	0.79	0.765	6.87*	0.005	6.87*
" " *f*	log P = 2.560 + 1.429 log A	64	0.86				
" " *m*	log P = 2.533 + 1.507 log A	58	0.77	4.641	6.87*	0.094	6.87*
" " *f+m+i*	log L = 2.614 + 0.436 log A	188	0.87				
Lac St-Louis, *f+m+i*	log L = 2.604 + 0.454 log A	109	0.87	0.066	6.73*	0.853	6.73*
Lac St-François, *f+m+i*	log P = 2.537 + 1.469 log A	188	0.87				
Lac St-Louis, *f+m+i*	log P = 2.542 + 1.505 log A	109	0.86	4.592	6.73*	0.531	6.73*

1. La croissance en longueur et en poids est identique chez les mâles et les femelles du lac Saint-François. On peut donc réunir ensemble les données des Maskinongés des deux sexes du lac Saint-François et nous supposons qu'il en est de même pour les autres lacs.

2. La croissance en longueur et en poids est identique chez les Maskinongés du lac Saint-François et du lac Saint-Louis. On peut donc grouper tous les Maskinongés mâles et femelles des lacs Saint-François et Saint-Louis en un seul ensemble; l'équation logarithmique de la croissance en longueur sera de la forme:

$$\log L = 2.608 + 0.446 \log A$$

et celle de la croissance en poids:

$$\log P = 2.526 + 1.499 \log A.$$

Nous allons pouvoir décrire ainsi la croissance en longueur et en poids des Maskinongés de ces deux lacs et ensuite la comparer avec celle des Maskinongés des lacs Ouareau et Saint-Joseph.

CROISSANCE EN LONGUEUR DES MASKINONGÉS EN PROVENANCE DES QUATRE LACS PROSPECTÉS

LACS SAINT-FRANÇOIS ET SAINT-LOUIS

Le Tableau II illustre la croissance en longueur des Maskinongés de ces deux lacs de la région de Montréal. La méthode du rétrocalcul propor-

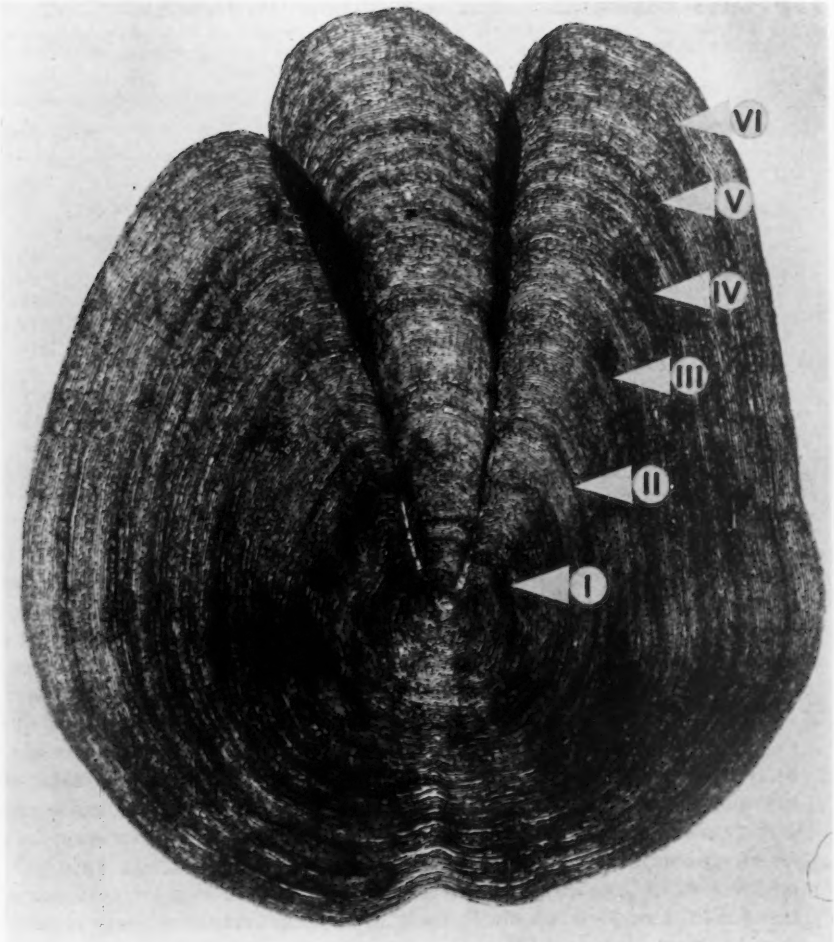

FIG. 2. Écaille d'un Maskinongé femelle capturé le 27 août 1948 dans le lac Saint-Louis. Ce poisson appartenait au groupe d'âge VI. Il mesurait 956 mm et pesait 5216 g. Le plus grand diamètre de cette écaille est de 8 mm.

Scale of a female maskinonge captured August 27, 1948 in Lake Saint-Louis. This fish belonged to age-group VI. It measured 956 mm and weighed 5216 g. The largest diameter of this scale is 8 mm.

TABLEAU II. Longueurs moyennes ($\bar{L}$) et extrêmes en millimètres aux différents groupes d'âge des Maskinongés des lacs Saint-François et Saint-Louis. Les longueurs aux groupes d'âge marqués d'un astérisque ont été obtenues par rétrocalcul proportionnel. Pour les autres groupes d'âge, il s'agit des moyennes et des extrêmes des mesures effectuées sur les spécimens récoltés. L'intervalle de confiance sur les valeurs individuelles est calculé pour un niveau de probabilité de 5% (I.C. 5%).
Average lengths ($\bar{L}$) and maximum length in millimeters of the different age-groups of maskinonge of lakes Saint-François and Saint-Louis. The lengths of the age-groups marked with an asterisk (*) were obtained by proportional back-calculation. The lengths of the other age-groups were obtained by measurement of the collected species. The confidence interval in the individual values is calculated for a level of probability of 5% (I.C. 5%).

Groupe d'âge	N	$\bar{L}$	I.C. 5%	Extrêmes
I*	64	184		124–291
II*	64	402		295–622
III	13	657	560–755	540–700
IV	34	756	669–860	624–870
V	53	833	746–921	736–959
VI	56	914	808–1020	791–1050
VII	40	968	818–1118	848–1244
VIII	37	1041	927–1155	940–1168
IX	22	1055	937–1173	939–1156
X	11	1112	939–1286	1010–1216
XI	11	1174	999–1349	1092–1327
XII	12	1239	1072–1045	1135–1358
XIII	3	1232		1219–1257
XIV	3	1290		1274–1321

tionnel à partir des écailles a été utilisée pour calculer les longueurs des poissons dans les groupes d'âge où l'effectif était trop faible. Elle a été utilisée dans le cas des lacs Saint-François et Saint-Louis pour établir les longueurs des spécimens des groupes d'âge I et II; nous avons utilisé les écailles des spécimens des groupes d'âge IV et V de façon à éliminer l'erreur que l'on risquerait de faire à partir de sujets plus âgés (phénomène de Lee).

On remarque que les Maskinongés d'un même groupe d'âge ont des tailles très différentes et que les intervalles chevauchent largement d'un groupe d'âge à l'autre. Il s'agit là d'un phénomène qui s'observe souvent chez les poissons: ces variations reflètent leur grande variabilité phénotypique.

On peut maintenant décrire le déroulement et les variations de croissance des Maskinongés des lacs Saint-Louis et Saint-François. Ils grandissent très vite la première année, puisque le jeune alevin qui a 11 mm à l'éclosion et 14 mm à la fin de l'absorption du sac vitellin (Fish, 1932) atteint 50 mm à la fin de juin, et 100 mm à la fin de juillet (Fry et al., MS, 1941). A la fin de l'été qui a suivi leur éclosion, les Maskinongés de la région de Montréal ont une taille de 180–190 mm. Au groupe d'âge II, ils ont doublé leur longueur (400 mm) et au groupe III, elle est triplée (600 mm). Au groupe IV, le taux de croissance diminue un peu puisqu'ils ont une longueur moyenne de 750 mm; au groupe V, ils atteignent 800 mm; il leur faut donc 2 ans (III–V) pour quadrupler la longueur du groupe d'âge I. Au groupe d'âge VI, ils atteignent

900 mm et au groupe VIII, 1000 mm; il leur faut alors 3 ans (V–VIII), pour quadrupler la longueur du groupe d'âge I. Au groupe d'âge X, ils ont 1100 mm de longueur et au groupe XII, 1200 mm: donc 4 années (VIII–XII) sont nécessaires pour quintupler la longueur atteinte à 1 an. Au groupe d'âge XIV, ils ont 1300 mm.

LACS SAINT-JOSEPH ET OUAREAU

Les Maskinongés ont été introduits dans ces lacs en 1951. Les Tableaux III et IV illustrent la croissance en longueur des Maskinongés de ces deux

TABLEAU III. Longueurs moyennes ($\overline{L}$) et extrêmes en millimètres et poids moyens ($\overline{P}$) et extrêmes en grammes aux différents groupes d'âge des Maskinongés du lac Saint-Joseph. Les longueurs aux groupes d'âge ont été obtenues par rétrocalcul proportionnel. Les poids ont été obtenus par transposition des longueurs dans l'équation du poids en fonction de la longueur donnée dans le texte.

Average lengths ($\overline{L}$) and maximum lengths in millimeters and average weights ($\overline{P}$) and maximum weights in grams of the different age-groups of maskinonge of Lake Saint-Joseph. The lengths of the age-groups were obtained by proportional back-calculation. The weights were obtained by transposing the length in the equation (weight in function of the length) mentioned in the text.

Groupe d'âge	N	$\overline{L}$	Extrêmes	$\overline{P}$	Extrêmes
I	29	128	50–181	29	2–61
II	29	384	195–591	573	73–1679
III	29	600	438–685	1825	716–2819
IV	23	752	618–846	3358	1884–4592
V	11	836	719–963	4539	2911–6653
VI	7	907	775–967	5700	3590–6699
VII	4	934	819–989	6168	4188–7145
VIII	3	967	857–1028	6828	4776–7980
IX	3	991	882–1045	7292	5165–8353
X	3	1011	908–1062	7690	5611–8730

lacs. La méthode du rétrocalcul proportionnel a été utilisée intégralement pour déterminer les longueurs des spécimens aux différents groupes d'âge; ceci était rendu nécessaire à cause de l'effectif réduit.

On remarque que la croissance en longueur est très différente dans ces deux milieux: dans le lac Saint-Joseph la croissance en longueur est rapide au cours des quatre premières années, elle diminue alors brusquement et du groupe d'âge V au groupe d'âge X l'augmentation en longueur se fait très lentement. Dans le lac Ouareau la croissance en longueur est rapide au cours des cinq premières années, elle diminue ensuite et on observe ici aussi une très faible augmentation de la longueur du groupe VI au groupe X.

COMPARAISONS DE LA CROISSANCE EN LONGUEUR DANS LES QUATRE LACS

La Fig. 3 illustre les différences de croissance en longueur des Maskinongés en provenance des quatre lacs prospectés. Nous avons porté, dans cette

TABLEAU IV. Longueurs moyennes ($\overline{L}$) et extrêmes en millimètres et poids moyens ($\overline{P}$) et extrêmes en grammes aux différents groupes d'âge des Maskinongés du lac Ouareau. Les longueurs aux groupes d'âge ont été obtenues par rétrocalcul proportionnel. Les poids ont été obtenus par transposition des longueurs dans l'équation du poids en fonction de la longueur donnée dans le texte.

Average lengths ($\overline{L}$) and maximum lengths in millimeters and average weights ($\overline{P}$) and maximum weights in grams of the different age-groups of maskinonge of Lake Ouareau. The lengths of the age-groups were obtained by proportional back-calculation. The weights were obtained by transposing the length in the equation (weight in function of the length) mentioned in the text.

Groupe d'âge	N	$\overline{L}$	Extrêmes	$\overline{P}$	Extrêmes
I	12	134	80–185	13	2–30
II	12	302	198–383	163	38–321
III	12	459	341–575	616	220–1208
IV	12	602	422–723	1487	439–2541
V	11	714	559–884	2538	1097–4074
VI	4	761	743–783	3013	2780–3304
VII	3	821	818–822	3846	3811–3864
VIII	3	855	850–861	4380	4296–4488
IX	3	878	867–888	4573	3954–4955
X	3	896	884–910	5102	4876–5371

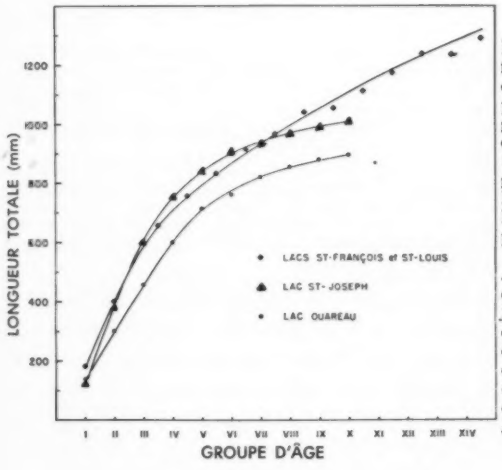

FIG. 3. Longueur moyenne aux différents groupes d'âge chez les Maskinongés provenant des quatre lacs prospectés. Les moyennes pour chaque groupe d'âge sont soit des moyennes de longueurs calculées par rétrocalculs (points correspondant aux différents groupes d'âge) soient des moyennes de longueurs des poissons au moment de la capture (points situés entre les groupes d'âge). Les courbes ont été tracées empiriquement.

Average length of the different age-groups among the maskinonge obtained from the four harvested lakes. The averages for each age-group are either average lengths determined by back-calculation (points corresponding to the different age-groups) or average lengths of the fish at time of capture (points situated between the age-groups). The curves were traced empirically.

figure, les moyennes des longueurs obtenues pour chaque groupe d'âge: pour les spécimens des lacs Saint-François et Saint-Louis, ce sont les moyennes des valeurs individuelles, tandis que pour les lacs Saint-Joseph et Ouareau, il s'agit des valeurs obtenues par rétrocalcul proportionnel. La similitude des courbes de croissance des Maskinongés des lacs Saint-Joseph et Ouareau est remarquable: à partir de III ans, les deux courbes sont parallèles. Ces courbes sont, par contre, très différentes de celle des lacs Saint-François et Saint-Louis.

Dans le lac Saint-Joseph la croissance en longueur, très rapide au départ, dépasse même, pour les groupes d'âge III, IV, V et VI, la croissance des Maskinongés des lacs Saint-François et Saint-Louis. La croissance est alors beaucoup plus lente et les individus des groupes d'âge VIII, IX et X ont une longueur moyenne inférieure à celle des individus de la région de Montréal.

Dans le lac Ouareau, la croissance en longueur des Maskinongés est toujours inférieure à celle des spécimens de la région de Montréal.

En comparant la croissance en longueur des Maskinongés du lac Saint-Joseph et du lac Ouareau, on s'aperçoit que les Maskinongés du lac Ouareau atteignent 600 mm au groupe d'âge IV, un an plus tard que ceux du lac Saint-Joseph; au groupe d'âge VI, leur taille est de 750 mm, 2 ans plus tard; au groupe d'âge VII, 820 mm, 3 ans plus tard; au groupe X, 900 mm, 4 ans et demi plus tard. La croissance en longueur des Maskinongés est donc beaucoup plus lente dans le lac Ouareau.

Croissance en poids des Maskinongés en provenance des quatre lacs

lacs saint-françois et saint-louis

Le Tableau V illustre la croissance en poids des Maskinongés de ces deux lacs. Sur ce tableau apparaissent les valeurs moyennes et les intervalles de

Tableau V. Poids moyen ($\overline{P}$) et extrêmes en grammes aux différents groupes d'âge des Maskinongés des lacs Saint-François et Saint-Louis. Les poids aux groupes d'âge marqués d'un astérisque ont été obtenus par transposition des longueurs dans l'équation du poids en fonction de la longueur donnée dans le texte. Pour les autres groupes d'âge, il s'agit des moyennes et des extrêmes des mesures effectuées sur les spécimens récoltés. L'intervalle de confiance sur les valeurs individuelles est calculé pour un niveau de probabilité de 5% (I.C. 5%).

Average weight ($\overline{P}$) and maximum weights in grams of the different age-groups of maskinonge of lakes Saint-François and Saint-Louis. The weights of the age-groups marked with an asterisk(*) were obtained by transposing the length in the equation (weight in function of the length) mentioned in the text. For the other age-groups the average and maximum measurements were completed on the collected specimens. The confidence interval in the individual values is calculated for a level of probability of 5% (I.C. 5%).

Groupe d'âge	N	$\overline{P}$	I.C. 5%	Extrêmes
I*	64	28		7–112
II*	64	358		118–1,410
III	13	1,598	857–2,339	907–2,041
IV	34	2,755	1,530–5,980	1,360–3,628
V	53	3,905	2,308–5,502	2,721–7,350
VI	56	5,279	2,768–7,790	2,840–9,080
VII	40	6,381	3,538–9,224	3,628–10,829
VIII	37	8,101	4,906–11,296	5,896–12,750
IX	22	8,950	5,269–12,631	6,803–12,473
X	11	10,490	5,917–15,063	8,306–14,288
XI	11	11,404	8,215–14,593	8,845–12,700
XII	12	13,333	7,683–18,983	10,149–16,782
XIII	3	13,683		10,432–18,597
XIV	3	14,363		14,061–14,514

confiance pour les valeurs individuelles. Les poids des groupes d'âge I et II ont été obtenus par transposition des longueurs, obtenues par rétrocalcul proportionnel, dans l'équation qui exprime la relation existant entre la longueur et le poids des Maskinongés des lacs Saint-François et Saint-Louis:

$$\log P = -6.179 + 3.341 \log L.$$

Le tableau montre que les fluctuations du poids sont beaucoup plus grandes que celles de la longueur et que les intervalles chevauchent très largement d'un groupe d'âge à l'autre.

LACS SAINT-JOSEPH ET OUAREAU

Les Tableaux III et IV illustrent la croissance en poids des Maskinongés des lacs Saint-Joseph et Ouareau. Afin d'établir la croissance en poids des Maskinongés de ces deux lacs, nous avons utilisé la relation mathématique qui existe entre la longueur et le poids des spécimens recueillis. Pour les Maskinongés du lac Saint-Joseph:

$$\log P = -4.598 + 2.822 \log L;$$

pour ceux du lac Ouareau:

$$\log P = -5.907 + 3.257 \log L.$$

Connaissant la longueur d'un spécimen, aux différents groupes d'âge, longueur obtenue précédemment par rétrocalcul proportionnel, il est donc possible de connaître le poids de ce spécimen au moment de la formation des divers annuli.

COMPARAISONS DE LA CROISSANCE EN POIDS DANS LES QUATRE MILIEUX

La Fig. 4 illustre les différences de croissance en poids des Maskinongés en provenance des quatre lacs prospectés. Son examen permet de constater ici aussi la similitude d'allure des courbes de croissance en poids des Maskinongés des lacs Saint-Joseph et Ouareau. La croissance en poids est plus rapide au départ dans le lac Saint-Joseph par rapport à celle des Maskinongés des autres milieux; elle devient inférieure cependant à partir du groupe d'âge VII à la croissance en poids des individus de la région de Montréal.

COMPARAISONS AVEC LES DONNÉES DE LA LITTÉRATURE ET CONCLUSION

La croissance des Maskinongés a été décrite de plusieurs façons par les différents auteurs: certains utilisent, par exemple, la longueur à la fourche; d'autres expriment les longueurs en pouces ou les poids en livres. Il nous a fallu faire les conversions nécessaires pour exprimer la longueur totale en millimètres et le poids en grammes.

La croissance du Maskinongé l'année de son éclosion fut décrite en particulier par Elson (1940), en Ontario, d'après des spécimens capturés de mai

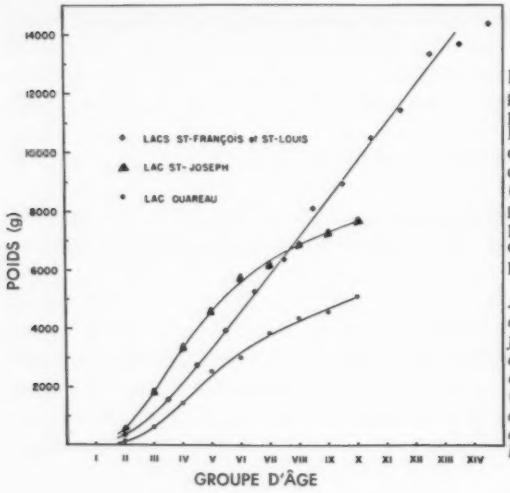

FIG. 4. Poids moyen aux différents groupes d'âge chez les Maskinongés provenant des quatre lacs prospectés. Les moyennes pour chaque groupe d'âge sont soit des moyennes calculées comme on l'a indiqué dans le texte (points correspondant aux différents groupes d'âge) soient des moyennes de poids des poissons au moment de la capture (points situés entre les groupes d'âge). Les courbes ont été tracées empiriquement.

Average weight of the different age-groups among the maskinonge obtained from the four harvested lakes. The averages for each age-group are either averages calculated as indicated in the text (points corresponding to the different age-groups) or average weights of the fish at time of capture (points situated between the age-groups). The curves were traced empirically.

à novembre. Ses résultats sont très proches de ceux de Fry et al. (MS, 1941), obtenus d'après de jeunes spécimens du lac Saint-Louis.

Le premier auteur qui s'est intéressé à la croissance du Maskinongé fut probablement Moore (1926). Cet auteur présente les données de 20 spécimens du lac Chautauqua, état de New-York; ses résultats correspondent à ceux que nous avons obtenus sur les Maskinongés de la région de Montréal: un poisson de 12 ans, par exemple, mesurait 1282 mm et pesait 16,329 g.

Les Maskinongés du lac Donaldson (Couture, 1964), ont une croissance semblable à ceux des lacs Saint-François et Saint-Louis; ceux du ruisseau Nogies (Muir, 1960) ont été capturés à l'automne et au printemps; l'auteur a décalé d'un groupe d'âge les individus capturés au printemps: c'est ce qui explique la longueur étonnante des Maskinongés du groupe d'âge I (403 mm), qui ont en fait au moins deux périodes complètes de croissance estivale. La croissance est cependant inférieure à celle des spécimens des lacs Saint-François et Saint-Louis, surtout, à partir du groupe d'âge IV.

Les spécimens de l'ouest ontarien (Hourston, MS, 1949 et 1952) ont été capturés au cours de l'été: les longueurs et les poids moyens sont inférieurs à ceux des Maskinongés de la région de Montréal et se rapprochent fort des mesures moyennes des spécimens du lac Ouareau.

En Pennsylvanie (Buss et Miller, 1961) et au Wisconsin (Schloemer, 1936; Juday et Schloemer, 1938), la croissance des Maskinongés s'effectue de facon très semblable à celle des spécimens de la région de Montréal.

Muir (1960) trouve une différence marquée de croissance en longueur entre les Maskinongés indigènes et les Maskinongés introduits dans un même lac. Les poissons introduits ont une taille plus grande que celle des Maskinongés indigènes au cours des quatre premiers étés; après cela, la croissance di-

minue rapidement et les deux courbes se coupent à la fin du groupe d'âge III. On peut rapprocher ces deux types de croissance des deux types que nous avons observés chez les Maskinongés introduits du lac Saint-Joseph d'une part et chez les Maskinongés indigènes des lacs Saint-François et Saint-Louis d'autre part (Fig. 3); la différence que l'on observe dans ces deux courbes de croissance ne serait pas due au fait que les deux types de lacs sont différents mais uniquement au fait que dans l'un des Maskinongés ont été introduits alors que dans l'autre il s'agit d'une population autochtone. Cela semble être confirmé par l'examen de la croissance des Maskinongés du lac Ouareau, croissance qui a la même allure générale que celle des Maskinongés du lac Saint-Joseph. Ce phénomène se retrouve d'ailleurs chez d'autres poissons. Crossman et Larkin (1959) ont en effet, fait des observations semblables chez des populations naturelles et introduites de *Salmo gairdneri* dans un même lac; jusqu'au groupe d'âge III, les truites arc-en-ciel provenant d'une pisciculture atteignent des tailles plus grandes que les truites indigènes; cette étude cependant ne fournit pas de renseignements sur les poissons plus âgés.

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Nous désirons exprimer d'une facon toute particulière notre gratitude à M. V. Legendre qui nous a fourni une documentation précieuse sur le sujet et des collections considérables de données récoltées en 1940–61 par l'Office de Biologie du Ministère de la Chasse et des Pêcheries du Québec, ainsi qu'à M. le Professeur P. Jolicoeur du Département de biologie de l'Université de Montréal qui nous a fait profiter de son expérience et de ses conseils dans l'analyse biométrique des données.

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The Mio-Pliocene Pinniped *Imagotaria*[1]

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ABSTRACT

The new genus and species *Imagotaria downsi* is described from Mio-Pliocene rocks in coastal southern California and a new subfamily proposed to receive it, the Imagotariinae. The new species was too specialized to have given rise to any living pinniped. It had large lingual, cingular cusps on the postcanine teeth and a vagina processus styloidei, for reception of the hyoid arch into the confines of the auditory bulla, enlarged to a degree not found in living sea lions. Related more closely to walruses and early otariids than to living sea lions, *I. downsi* evidently represents an evolutionary line independently attaining the structural grade of sea lions through parallel evolution from an early common ancestor.

The middle ear region is described in detail and some anatomical terms are defined in order to more fully emphasize basicranial structures. A referred specimen from the same geologic unit, the Sisquoc Formation, is mentioned and the distribution of *I. downsi* and related species in time and space is discussed.

Comparisons of the skull, dentition, and especially the middle ear region are presented and a discussion of the present state of knowledge of otariid phylogeny emphasizes that many different kinds of otariids have existed in the past. Not all of these can easily be called walruses or sea lions. The wide adaptive spectrum now known within Otariidae is comparable to that within Phocidae.

Diagnoses of subfamilies are given based upon basicranial features, and a provisional classification is offered. The Otariidae is revised to include: the old family Odobenidae as a subfamily; the subfamilies Desmatophocinae, Allodesminae, Dusignathinae, Imagotariinae, and Otariinae (including the old subfamily Arctocephalinae as a tribe). These subfamilies are diagnosed on the basis of many basicranial features newly found to be of importance in otariid systematics.

A survey of putative North Pacific extinct Otariini suggests: *Pontolis magnus* is too specialized to be considered as an ancestor of *Eumetopias*; the "cf. *Pontolis magnus*" of Lyon (1941) is possibly a species of *Pontolis*; *Eumetopias sinanoensis* Nagao (1941) is a junior synonym of *Allodesmus kernensis* Kellogg (1922); a new genus *Oriensarctos* is proposed to receive the species *Eumetopias watasei* Matsumoto (1925); the "*Allodesmus* sp" of Kaseno (1951) is *Eumetopias* sp; and *Eumetopias* (?) *kishidai* Shikama (1953) is relegated to synonymy under *Zalophus californianus* (Lesson, 1828).

Imagotaria downsi is related to *Pontolis*, and possibly more closely to *Phocarctos hookeri* and other southern hemisphere Otariini than to living northern Pacific species of Otariini. It is a relative of *Desmatophoca oregonensis*, descended from that or a related species and paralleling living sea lions.

INTRODUCTION

A new kind of sea lion has been discovered in Mio-Pliocene diatomites in the southern California region. With the description below of a new species of otariid pinniped, information becomes available to emphasize the diversity of sea lions, and derive a synthetic picture of late Tertiary otariid radiation.

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This diversity is recognized herein in the proposal of new subfamilies and the definition of other subfamilies previously recognized on the same or a different rank. A survey of North Pacific fossil Otariini has resulted in the proposal of a new generic name for a previously described species, the synonymizing of two species from Japan, and the reinterpretation of other described fossils. This study is part of a series on the biology of extinct pinnipeds: some papers (Mitchell, 1961, 1966a) are oriented towards species, others (Mitchell, 1962, 1965, 1966b) towards faunal assemblages containing pinnipeds. Papers are in preparation on the Miocene pinniped *Desmatophoca* and the Pliocene pinnipeds *Pontolis* and *Dusignathus*.

On the basis of numerous major features, living pinnipeds have been conveniently divided into true seals (Phocidae) and fur seals, sea lions, and walruses (Otariidae and Odobenidae). The Otariidae have been further divided into sea lions (Otariidae: Otariinae) and fur seals (Otariidae: Arctocephalinae), divisions reflecting relatively recent evolutionary separation. The ancestry of walruses is surmised to have stemmed from primitive and generalized sea lions (True, 1912, p. 199), the origin of fur seals certainly predates the Late Miocene as a fur seal of that age has been described (Kellogg, 1925a), arising from or with sea lions from an earlier stock and the Otariinae were thus probably also distinct before that time. In the North Pacific basin, reputedly the center of origin and certainly the center of dispersal of most otariids, the fossil record of the Otariinae is incomplete. A number of extinct species have been described, the oldest of which is reputedly *Pontolis magnus* from the Pliocene of coastal Oregon. True (1905a, b, 1909) concluded that *P. magnus* was very close to, if not the actual ancestor of, *Eumetopias jubata*.

From this point on within this paper I shall refer to the various groups of eared pinnipeds (my newly recognized Otariidae, sensu lato) in the terminology defined in the Classification presented near the end of the paper. Thus I will speak of the Otariini and the Arctocephalini but both are included in the term otariine. In the past the Otariinae has referred to only the living sea lions, but I now lump living fur seals with them in the new, expanded Otariinae.

The contents of this paper are organized in the following manner: description of the holotype of *Imagotaria downsi*; description of the referred specimen of *I. downsi* from Lompoc diatomites; distribution of the species and close relatives; comparison of the new species with living Otariini; comparison with other living Otariidae (Arctocephalini and *Odobenus rosmarus*); comparison with extinct Otariini and reputed Otariini; comparison with selected other extinct Otariidae (the ear regions of *Desmatophoca oregonensis* holotype, *Dusignathus santacruzensis* holotype, and *Allodesmus kelloggi* holotype); Otariid phylogeny; Otariid subfamilies and their diagnoses; and provisional otariid classification.

DESCRIPTIONS

Imagotaria downsi new genus and species

The holotype of this species is SBMNH 342, numerous elements from the anterior half of an associated skeleton of an adult sea lion including: a nearly

complete palate, right dentary and fragments of the left, portions of the left temporal bone, the atlas, both glenoid fossae of the scapulae, major portions of both left and right humeri, isolated teeth, and other cranial and postcranial fragments. Though not complete, this skeleton includes such material critical in comparisons as the palate and mandibles with dentition, the middle ear region, and the humerus. These bones were collected by Phil C. Orr from a "quarry of the Great Lakes Carbon Co. at Lompoc, California," but no more locality data is available. Orr has written (March 23, 1968): "I would say there is every possibility these come from a single individual from the circumstances of their discovery all within a few feet square, with no other bones of any kind being found for 50 or more feet around as exposed by bulldozers and carefully checked over by myself and museum assistant as well as several quarry workmen." The diatomites in his region are part of the Sisquoc Formation of the Early Pliocene or Late Miocene (see Dibblee, 1950).

The species based upon the SBMNH[2] skeleton is named *downsi*, for Dr Theodore Downs in appreciation of his contributions to knowledge of pinniped history, and is the type species of the genus *Imagotaria*.

The latter is derived from the generic name *Otaria* (a Greek name for the type genus of the family Otariidae) and the Latin *imago*, the thing produced in an act of imitation, thus an imitation sea lion not ancestral to living species but paralleling them.

The diagnosis covers a number of features necessary in order to compare the holotype with disparate material from other poorly or incompletely known extinct species. In the diagnosis below, and the diagnoses of the subfamilies presented near the end of this paper, major features are in italic type for ease of comparison but the remaining characters are also trenchant.

Diagnosis. — An otariid pinniped sensu Scheffer (1958), Mitchell (1966a) with an arched palate; upper dentinal formula I1/-I2/-I3/-C1/-PC1/-PC2/-PC3/-PC4/-PC5/-?; lower formula I/1-I/2-?-C/1-PC/1-PC/2-PC/3-PC/4-PC/5-PC/6; *most postcanine teeth incipiently double rooted, with vertical sulcus on labial surface of root; postcanine crowns with enlarged lingual cusp on lingual cingulum*; lower cheek teeth aligned on straight axis; masseteric fossa not well delimited; lambdoid crest high and sharp; *auditory bulla smooth and flat; apical bullar spur and fossa present; posterior bullar projection present*; external auditory meatus not cylindrical, directed laterally, formed by squamosal dorsally, post-glenoid buttress anteriorly, mastoid posteriorly, and tympanic ventrally; no suprameatal fossa; inferior edge of external auditory meatus spinose; basioccipital enters into carotid canal wall posteromedially; *paroccipital process thin, plate like; paroccipital and mastoid processes united by ridge of bone broadly continuous, directed ventrally*; postglenoid foramen large; canalis caroticus enclosed entirely within tympanic, except basioccipital contributing to posterointernal wall; posterior carotid foramen large, opening ventroanteriorly to and separate from posterior lacerate foramen; foramen lacerum posterius small; sphenoid contributing to internal carotid canal wall dorsoanterolaterally; foramen stylomastoideum between bulla and mastoid; *vagina processus styloidei present, separate from but connecting with foramen stylomastoideum only via an elongate canal behind bulla*; posterior bullar projection and labrum vagina pro-

[2]Nomenclature of living species in this report generally follows that of Scheffer (1958). Abbreviations used include: BM(NH), British Museum (Natural History); LACM, Los Angeles County Museum of Natural History; SBMNH, Santa Barbara Museum of Natural History; UCMP, University of California Museum of Paleontology, Berkeley; UOMNH, University of Oregon Museum of Natural History; USNM, United States National Museum; UW, University of Washington.

cessus styloidei project posteriorly from bulla; paroccipital process not touching bulla; no pterygoid contact with bulla; basisphenoid probably touches bulla; bulla and mastoid fused between paroccipital process and foramen stylomastoideum; hyoid arch may lie in ectotympanic or between entotympanic and ectotympanic; auditory cavity long, narrow, and deep, bounded by entotympanic, ectotympanic, pars petrosa, pars squamosa, pars mastoidea?, sphenoid, tympanohyal; auditory cavity not extending into surrounding elements; no mastoid contribution to auditory cavity wall internal to eminentia vagina processus styloidei; foramen magnum bullae medium size; foramen pneumaticum large; no epitympanic sinuses; hypotympanicum large, inflated medially and ventrally well beyond promontorium; *pronounced eminentia vagina processus styloidei on posterior wall of hypotympanicum*; no septum bullae; recessus meatus acousticus externi small; *crista tympani projected into auditory cavity, without free ventral edge*; primary tympanic cavity small relative to hypotympanicum; canalis caroticus almost touches fenestra cochleae; canalis caroticus underlain by hypotympanicum posteriorly; tympanohyal enclosed within vagina processus styloidei at level of membrana tympanica, fused in with wall of auditory cavity; struts on external wall radiate from crista tympani; membrana tympanica oriented ventrointernally 60° from axis of meatus acousticus externus; ossified ring not completely fused to crista tympani in sulcus tympanicus; *sulcus tympanicus horseshoe shaped, longest diameter anteroposterior*; recessus epitympanicus pear shaped, relatively small, bounded mainly by pars petrosa and pars squamosa, with narrow fossa incudis; *septum canalis musculotubarii a thin, cylindrical shell of ectotympanic, tube like, almost but not contacting dorsal roof of auditory cavity*; promontorium low, rounded, bulbous, and inflated only posteriorly, base triangular in shape with one apex posteriorly; fenestra cochleae huge, facing posterointernally; secondary tympanic membrane in vertical plane oriented 40° anterointernally from transverse axis; perilymphatic duct opens intracranially on line between meatus acousticus internus and hiatus petrotympanicus; fenestra vestibuli in oblique, ventrointernal plane parallel to long axis of skull; ramus tympanicus of nervus glossopharyngeus, and tympanic plexus run in grooves on promontorium ventral to fenestra vestibuli; ramus auricularis of nervus vagus passes transversely, dorsoposterior to tip of tympanohyal; geniculum nervus facialis at level of posterior end of septum canalis musculotubarii, bony analogue of "Chordafortsatz" of Bondy small; *pars petrosa not excavated for canalis petrobasilaris, bulbous internally*; tympanic wall of canalis caroticus may not contribute to wall of canalis petrobasilaris; dorsal region of pyramid striated slightly, flattened, defined from globous ventral region of pyramid by distinct sulcus; *distinct bony trough around aqueductus cochleae projected internally into cranial cavity*; *fossa cerebellaris deeper than transverse width of entrance*; *tentorium appressed to external side of canalis semicircularis ossei anterior*; *fovea dentis of atlas concavely excavated*; *coracoid process of scapula enlarged*; *diameter of capitulum large*, 32% of functional humeral length; greater tuberosity higher than lesser, high and thin; deltoid tuberosity incorporated into deltoid crest; *humeral shaft relatively straight*; *dorsal surface of entepicondyle directed internally*.

Description and comparisons: *palate and teeth*. — Much information can be derived from the palate (SBMNH 342a, Fig. 1, 2) even though it is broken and slightly distorted. The individual is large, most sutures are fused, or tightly appressed, but the roots of the canines show an open pulp cavity. It is compared throughout with adults and subadults of other species where possible. The palatal roof is transversely arched in its anterior portion to a greater extent than in *Eumetopias* but not so much as in *Otaria*. More posteriorly, the palate flattens out as in *Eumetopias* but is wider. The incisive foramina are intermediate in size and shape between those of *Eumetopias* and *Otaria*. The median septum between these foramina is thin and compressed, neither thickened as in *Otaria* nor separated to form a double wall as in *Eumetopias*. The anterior margins of the foramina are narrow and well defined, extending to less than 8 mm behind the medial incisors. Within the narial chamber the internal or dorsal openings of the incisive foramina are narrow and the maxillary capsule for the base of the canine is smooth on its medial surface: both features are found in *Zalophus* and *Otaria* but not in *Eumetopias*. The rostral tuberosity is smooth and uniform, contrasting to the bifurcate condition in most other Otariini. There is no spur on the anteroventral border of the narial opening. The palatine bones have much the same distribution and shape as in *Zalophus*: the anterior or transverse maxillopalatine suture is straight, not

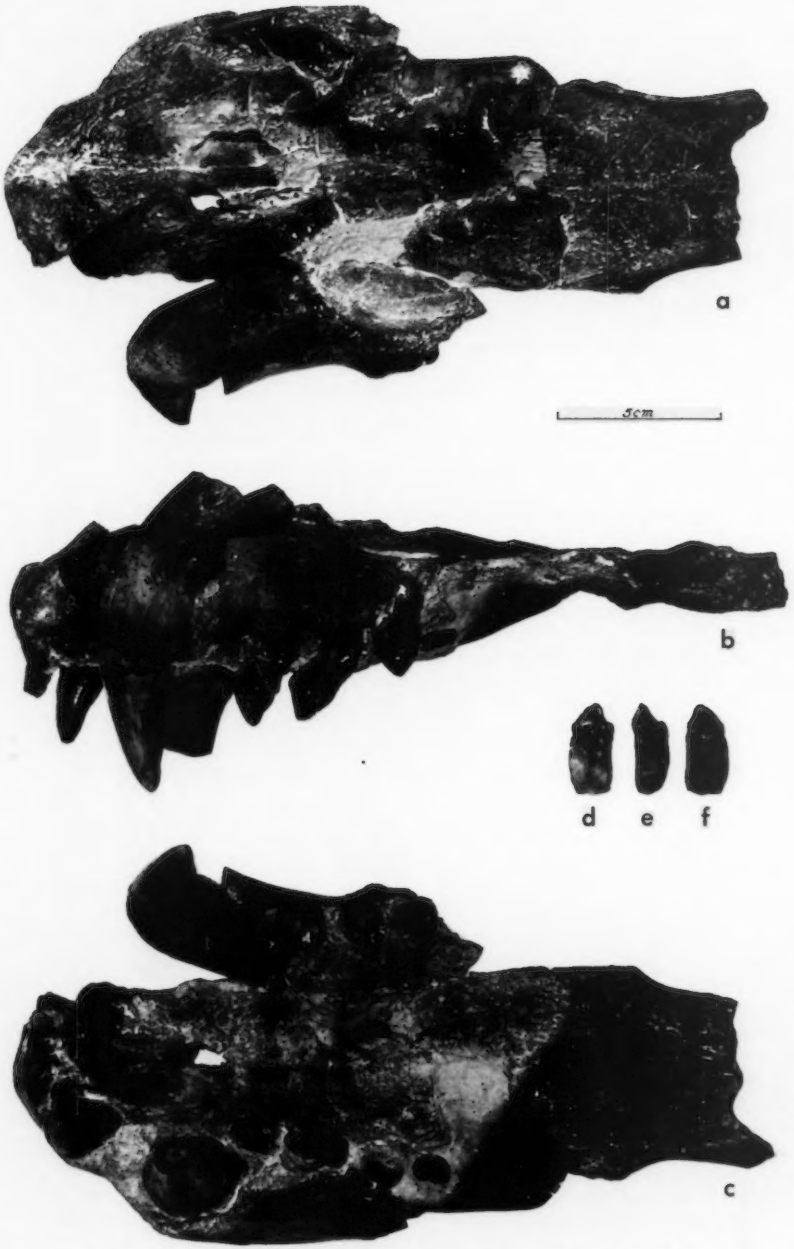

FIG. 1. Holotype of *Imagotaria downsi* new genus and species (SBMNH 342) from Late Miocene or Early Pliocene Sisquoc Formation near Santa Barbara, southern California. All views approximately one half natural size, scale is 5 cm long. Photos by Mike Hatchimonji. *a*, *b*, *c*, dorsal, left lateral, and ventral views of rostral portion of skull; *d*, *e*, *f*, external, posterior, and internal views of right upper postcanine four.

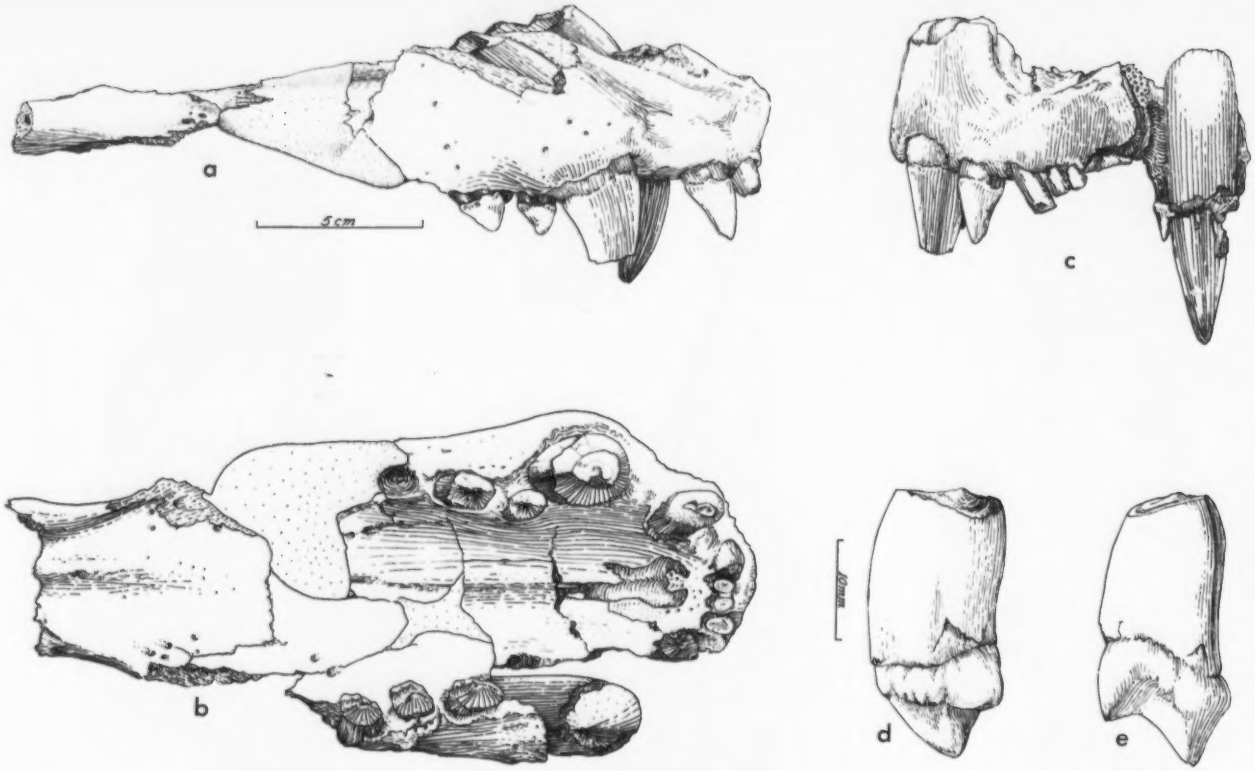

FIG. 2. Holotype of *Imagotaria downsi* new genus and species (SBMNH 342) from Late Miocene or Early Pliocene Sisquoc Formation near Santa Barbara, southern California. All views approximately one half natural size, scale for rostal portion of skull is 5 cm long, for tooth is 10 mm. Orthographically projected drawings by Frank Paul. *a*, *b*, *c*, right lateral, ventral, and anterior view of rostral portion of skull (342a): *d*, *e*, lingual and posterior view of right PC4/ (342m).

rounded as in *Eumetopias* and *Otaria*. There is a slight ridge running down the middle of the palate.

There are three incisors: the lateral tooth (I3/) being large (18 mm in anteroposterior diameter and open rooted with a cingulum on the crown), I2/ being smaller (10 mm), and I1/ yet still smaller (7 mm) in diameter. The incisor tooth row is straight transversely as in most living, specialized otariines. The crowns are unfortunately not preserved. A diastema about 12 mm long separates the lateral incisor from the canine. The lateral incisor has a small cingulum posterolingually. The canine itself is large (30 mm in anteroposterior diameter), long (7 mm of root and 45 mm of well-enameled crown exposed above the alveolus), and is open rooted. The base of the root is very thin-walled, and the pulp cavity extends well into the crown area of the tooth. The external surface of the root is longitudinally striated: the lateral side of the root is slightly concave, a shallow sulcus running the whole length to the crown, but the internal surface is convex. A ridge is developed on the posterior surface of the crown, making the crown teardrop shaped in cross section. There is a small lingual cingulum on the crown of the canine. The postcanine tooth row contains at least four large teeth, subequal in size, that are closely spaced. Additional teeth may have been present but the posterior alveoli are broken away.

There are five cheek teeth preserved in the palatal fragment (342a), PC1/–2/ on the right and PC2/–4/ on the left. An isolated tooth (342m) is readily identifiable as right PC4/ by comparison with the left PC4/ in situ. All of these cheek teeth have a vertical sulcus on the labial surface of the root, dividing the root into incipient anterior and posterior roots. The division is not complete in any of these teeth, particularly since the lingual surface of the root carries no comparable sulcus and is bowed inward or inflated. In a cross section through one of these roots, particularly that of a PC4/ where the condition is enhanced, the external sulcus is marked and the section is kidney shaped in appearance. The crowns of the first four cheek teeth bear a major cusp and immediately behind it is a suggestion (PC1/) or a definite spur (PC2/) of a posterior cusp. There is a distinctly demarcated lingual cingulum, represented by a slight bulge on PC1/ with a tiny cuspule posterolingually, to a series of small cingular cuspules culminated in a prominent posterolingual cusp on PC4/. Wear surfaces between the main cusp on the crown and the posterolingual cingular cusp indicate that the lower and upper teeth occlude tightly. There are wear surfaces also on the tips of the main cusps of these upper teeth. On PC2/ there is a very small labial cingulum on the posterior end of the crown.

An isolated fragment of bone (342d) was found to fit the palate as a small part of the vomerine trough.

The fragment from the left maxillary bone (342e) shows the proximal end of the alveolus for the left upper canine to be pierced by numerous small foramina about 0.5 mm in diam. The shape and relations of the premaxillary–maxillary suture and internal narial wall are similar to those in most Otariini.

Mandible. — The mandible (Fig. 9, 10) is very similar to mandibles of Otariini, but differs in having a single rooted PC/6 whereas *O. byronia*, *Z. californianus*, and *E. jubata* have lost the PC/6 entirely. (It is sometimes present as an individual variation.) The lower teeth are not preserved in the jaw, but the alveoli indicate that PC/1 and PC/6 were single rooted and the remainder of the postcanines were incipiently double rooted. The lower border of the horizontal ramus of the mandible is arcuate from the genial tuberosity backwards. The anterior end of the mandible is very deep. There are three major mental foramina on the anterior end and two more smaller foramina beneath the canine and incisors, near the symphysis. The symphysis is rhombic in its posterior half, but probably rounded anteriorly, as viewed from the medial surface. Seemingly it is unfused, and both rami were separate. The ventral point of the symphysis is not the ventralmost point on the mandible, but is continuous with a roughened genial region that runs posteriorly on the ventral border of the ramus almost 4 cm. At the level of PC/6 the horizontal ramus is only 17 mm thick. The cheek teeth are aligned along a straight axis that runs from directly behind the canine to just internal to the ascending ramus of the mandible. The edges of the alveoli are sharp. The thickness of the alveolar septa range between about 1 and 2 mm; the entire cheek tooth row of 6 alveoli is 90 mm long. The root of PC/1 as judged from the alveolus was round, but PC/2–/5 had grooves on the external surface of the root. PC/5 seems to have been

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completely double rooted, but PC/6 was single rooted with a small round root. The root only remains in the alveolus of PC/2, and gross inspection suggests that there are growth zones in the cementum of the root. The canine, particularly on the lingual side, bears pronounced vertical striae on the enamel of the crown. The tip shows a small wear facet which runs down the posterior cutting edge about halfway the length of the crown. Below this, there is a weak but distinct cutting ridge. The isolated left canine (342h) shows a number of additional features. On both the internal and external surfaces of the root there is a small groove or sulcus, giving a cross section of the root at midlength a dumbbell shape. A distinct pulp cavity runs through the tooth up well into the crown, and is filled with diatomite matrix. There are no obvious cingula on the canines. There were at least two incisors in the lower jaw. An alveolus medial to the canine is approximately 5 mm in diam. The broken tip of a root about 6 mm in diam lies anterolaterally to this first alveolus. This region of the mandible is broken and the presence or undoubted absence of a third incisor cannot be resolved. Doubling the measurement for the right mandible, it would have been about 6.6 cm across the jaws at the level of the canines. The masseteric fossa is not well set off from the rest of the jaw. Its margins are indistinct and blend well with the surface of the horizontal ramus.

Two fragments from the left mandible include 342s, part of the body of the horizontal ramus, and 342r, the condyle. The condyle is about 60 mm across transversely, of which about 46 mm projects external to the midline of the vertical body of the mandible and about 14 mm projects internally. The condyle is about 19 mm in diam.

Two isolated teeth fit into the alveoli of the right lower mandible. On the basis of comparisons of two other isolated teeth with the first two, they can be allocated to positions in the fragmentary left mandible. The teeth are 342j, the crown and part of the root of right PC/3; 342l, complete right PC/5; 342i, crown and portion of the root of left PC/2; and 342k, crown and portion of the root of left PC/3. Based upon these teeth, the following description can be offered:

PC/1 is unknown. PC/2 has a sharp cutting ridge on both the posterior and anterior edges of the main cusp on the crown, and this ridge is continuous with the small but definite lingual cingulum. From a posterior view the main crown cusp is offset and lies over the external half of the root, with the cingular shelf lingually. PC/3 has a main cusp on the crown likewise offset labially. There is a very large anterior cusp as well, separated from the main cusp by a deep

TABLE I. Measurements of crowns, in millimeters taken parallel or perpendicular to the axis through the entire root, of postcanine teeth of holotype of *Imagotaria downsi* (SBMNH 342). Approximations are in parentheses.

	Length crown	Width crown
Upper		
Right PC 1	12.0	10.5
Left PC 2	14.0	11.0
Right PC 2	14.0	11.0
Left PC 3	14.8	11.5
Left PC 4	13.8	11.0
Right PC 4	12.5	11.4
Lower		
Left PC 2	13.0	10.0
Left PC 3	15.0	10.0
Right PC 3	15.1	10.0
Right PC 5	12.5	8.0

cleft. The tips of both these large cusps bear small wear facets. The posterior edge of the main cusp has a cutting edge that runs down and is continuous with a small posterior cingular cusp. The lingual cingulum is pronounced, sinuous in shape as viewed from the lingual side, and runs up the anterior cusp. The root is grooved only on the external side. PC/4 is unknown. PC/5 slants backward in its alveolus, is fully double rooted for about one third of its length, and has an anterior root that is longer than the posterior one. There is one low main cusp and an anterior and posterior minor cusp on the crown. All have wear surfaces on them, often continuous surfaces. The main crown cusp bears a posterolingual ridge, which is separated from the posterior accessory cusp by a small basin.

Isolated teeth and skull elements. — Two isolated teeth cannot be unquestionably allocated to positions in the jaws. The crown of one incisor (342o) probably represents a lower incisor, possibly the left outer incisor. The tip is worn and there is a fossa or sulcus in the supposed mediodorsal surface of the crown. Another small tooth, complete but for the broken root tip (342n), possibly represents the right lower PC/6. Alternatively it might represent one of the other last postcanine teeth in the upper or lower jaw.

A small sliver of bone (342b) might represent the left zygomatic process of the squamosal or a piece of the left jugal bone. If it does, it would demonstrate that the zygomatic arch was not so massive as in *Allodesmus kelloggi* but more like that of typical otariines.

TABLE II. Measurements in centimeters to nearest millimeter of skulls of *Imagotaria downsi* holotype (SBMNH 342), referred specimen (USNM 13487), and *Pontolis magnus* holotype (USNM 3792). Approximations in parentheses; asterisk denotes measurement by calculation of one-half width times two. Numbers are those of Sivertsen (1954).

	SBMNH 342	USNM 13487	USNM 3792
Total length, occipital condyles to tip of snout (0)	–	34.0	–
Width across braincase at level of anterior margin of glenoid fossae (8)	–	11.0	(11.5)
Posterior edge of upper incisors to palatal notch (10)	20.5	–	
Width across maxillae at canines (12)	(11.0+)	8.2	–
Thickness anteroposteriorly of inferior zygomatic root of maxillary (14)	–	(2.0)	–
Tip of snout to posterior border of postglenoid process (16)	–	26.0	–
Width across zygomatic arches (17)	–	17.2	–
Foramen magnum to infraorbital canal (18)	–	21.4	–
Auditory width (19)	–	(13.2)*	(20.8)
Mastoid width (20)	–	16.0	(24.2)
Paroccipital width	–	13.2	(21.9)
Foramen magnum to nearest point on anterior margin of glenoid fossa (21)	–	(11.0)	15.6
Width of palate between PC 1/	–	5.1	–
" " " PC 2/	5.4	5.2	–
" " " PC 3/	6.0	(5.0)	–
" " " PC 4/	(6.5+)	(5.0)	–
Snout tip to back edge of PC 1/	7.7	–	–
" " " " PC 2/	9.5	8.5	–
" " " " PC 3/	11.2	10.3	–
" " " " PC 4/	12.5	12.0	–
Breadth across outsides of infraorbital canals	–	8.7	–
Gnathion to end of maxillary (13)	18.8	–	–
Gnathion to anterior end of dorsal opening of incisive foramen in narial chamber	5.5	–	–

A large piece of the left lambdoid crest (342c) shows that the external surface of the left parietal was rather smooth, but had a fine lacework of reticulated ridges on its surface. The lambdoid crest is similar to that of adults of *Otaria byronia* and *Neophoca cinerea* (BM(NH) 1959.12.4.6 and 1925.10.8.32, respectively) but from a posterior view the crest is more rounded in the fossil and straighter across the top. The supraoccipital and parietal are well fused with no remaining vestige of a suture, and the crest is high and sharp. Clearly this animal had a high lambdoid crest as in some living Otariini.

Temporal bone. — The fragment of the left temporal bone (342f, Fig. 3) is comprised of the mastoid and paraoccipital processes, the auditory bulla, the middle and inner ear, and some adjacent structures. Most of the details discussed below are shown and labeled in Fig. 4–8. I prepared the fossil with a miniature sandblaster that removed relatively soft matrix from within canals and fossae but did not alter or damage the bone. Terminology follows that of Miller et al. (1964); van der Klaauw (1931); Gray (1954); and others. The following description of the ear region is very specific and detailed, and I have purposely given alternative terms for the same structure in order to aid comparisons with the pinnipeds and carnivores already mentioned in earlier literature. This essay will also serve to define my usage of terms to be applied in forthcoming descriptions of extinct pinnipeds. The discussion assumes that the structures are oriented as within a skull in a living animal.

The dorsal surface of the temporal bone is much damaged, missing much of the pars squamosa. The glenoid fossa is relatively large and composed of porous bone, with a postglenoid process extending down behind the mandibular condyle. The transverse axis of the glenoid fossa slants posterolaterally, toward the axis of the meatus acousticus externus with which it subtends an internal angle of about 23°. Medially the glenoid fossa terminates about 3 mm lateral to the sutura sphenosquamosa, which runs posteriorly and deeply into two foramina in a fissure just behind fissura petrotympanica. Within fissura petrotympanica, just anterolateral to the aforementioned pair of foramina, is another pair and farther laterally is a single, well-defined foramen postglenoideum. Behind the fissura petrotympanica and parallel to it is another crease, associated laterally with extensive vascularization. Behind the postglenoid process, laterally, is a single, large round foramen.

The postglenoid process forms the anterior, vertical wall of the meatus acousticus externus. The bridge of bone forming the dorsal roof of the meatus has upon its dorsal surface a slight ridge running anterointernally. The dorsal surface is continuous with the dorsum of the squamosal roof of the zygomatic arch anteriorly, and posteriorly ends abruptly at the mastoid crest. The massive mastoid process runs, in continuation from the thin lambdoid crest, ventrally and then is deflected mediposteriorly to meet the paroccipital process. Thus a large flange is formed by the mastoid with a small contribution from the occipital, the flange having a broad, smooth, and concave surface facing posterolaterally. The ventral border of the mastoid process is a broad rugose ridge up to 20 mm wide, with distinct boundaries. Howell (1929) figures the origin of musculus digastricus in *Z. californianus* from the entire paroccipital process and paroccipital–mastoid ridge, but this region is much reduced in *I. downsi*. The mastoid process is more than five times the length of the paroccipital–mastoid ridge. The exoccipital contribution to the paroccipital process, little more than a thin sheath covering the posterointernal edge of the huge mastoid flange, extends along the mastoid such that the sutura occipitomastoidea, from foramen lacerum posterius to the tip of the paroccipital process, is about 31 mm long. (In this paper my "paroccipital" or "paroccipital process" is the entire structural entity equivalent to the "paramastoid process" of some others, e.g. Chaine, 1922; but either term is misleading as the process, as for example in *Allodesmus kelloggi*, is a compound structure composed of both exoccipital and mastoid bone.)

The fragment of exoccipital bone preserved includes most of the paroccipital process and a bit of the wall of the cerebellar fossa. On line with the long axis of the paroccipital process, and dorsoexternal to the lip of the foramen lacerum posterius, the exoccipital articulates by means of a prominence with a socket in the pars petrosa of the temporal. The entire exoccipital contact with the mastoid is of the sutura harmonia type, simple contact of roughened surfaces. That part of the inferior border of the exoccipital making up the posterior lip of the foramen lacerum posterius is swollen into a thick ridge.

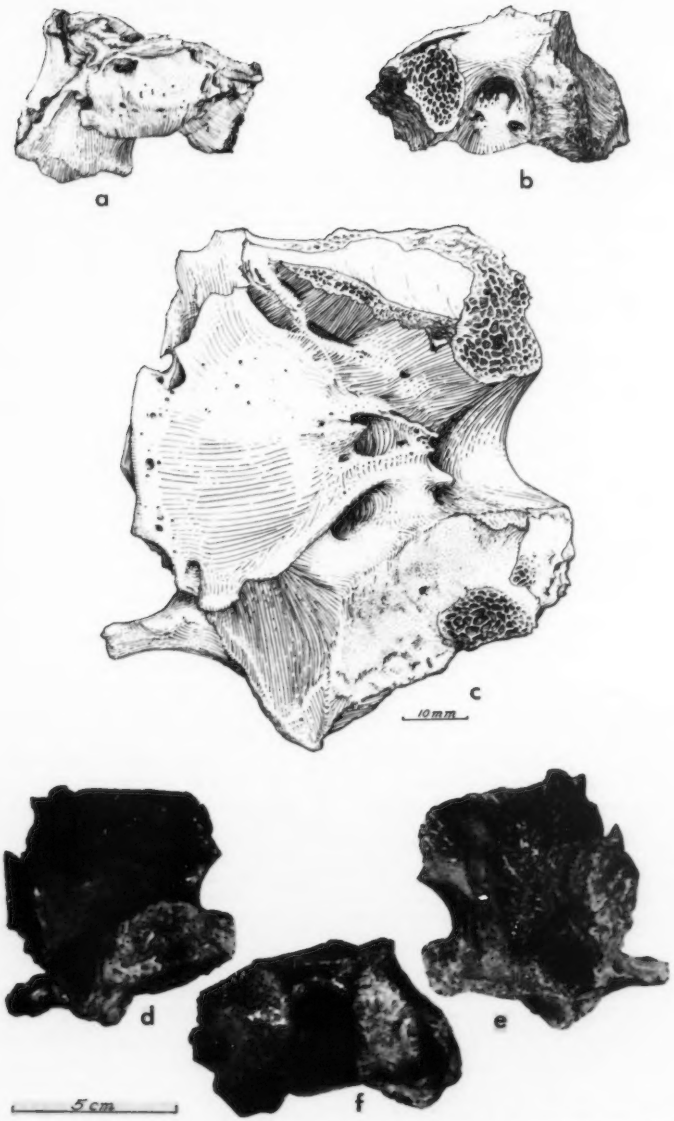

FIG. 3. Holotype of *Imagotaria downsi* new genus and species (SBMNH 342f) from Late Miocene or Early Pliocene Sisquoc Formation near Santa Barbara, southern California. Scale for all drawings and photographs except *c* is 5 cm long, scale for *c* is 10 mm long. Orthographically projected line drawings by Frank Paul, photographs by Mike Hatchimonji. *a*, *b*, *c*, internal, external, and ventral views of left temporal bone; *d*, *e*, *f*, ventral, dorsal, and external views of left temporal bone.

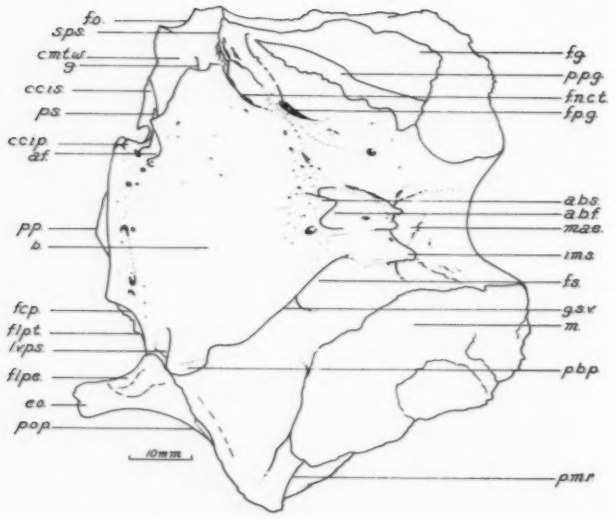

FIG. 4. Overlay of Fig. 3*c* giving details of basicranial structure of holotype of *Imagotaria downsi*. Scale is 10 mm long. Abbreviations: *a.b.f.*, apical bullar fossa; *a.b.s.*, apical bullar spur; *a.f.*, pit containing adventitious foramina; *b.*, smooth ventral surface of auditory bulla; *c.c.i.p.*, petrosal wall of canalis caroticus; *c.c.i.s.*, sphenoid wall of canalis caroticus; *c.m.t.w.*, dorsal roof of canalis musculotubarius formed by sphenoid bone; *e.o.*, exoccipital bone; *f.c.p.*, posteroventrolateral lip of foramen caroticum posterius; *f.g.*, fossa glenoideus; *f.l.p.e.*, exoccipital lip of foramen lacerum posterius; *f.l.p.t.*, tympanic lip of foramen lacerum posterius; *f.n.c.t.*, fissure between pars tympanica, sphenoid, and pars squamosa, in which lies foramen nervus chorda tympani; *f.o.*, posterior lip of foramen ovale; *f.p.g.*, foramen postglenoideum in fissura petrotympanica; *f.s.*, foramen stylomastoideum; *g.*, groove in roof of c.m.t.; *g.s.v.*, position of groove between foramen stylomastoideum and vagina processus styloidei; *i.m.s.*, inframeatal spine; *l.v.p.s.*, labrum vagina processus styloidei; *m.*, mastoid process; *m.a.e.*, meatus acousticus externus; *p.b.p.*, posterior bullar projection; *p.m.r.*, paroccipital–mastoid ridge; *p.o.p.*, paroccipital process of exoccipital; *p.p.*, pars petrosa or pyramid; *p.p.g.*, broken edge of processus postglenoideus; *p.s.*, processus styliformis between c.c. and c.m.t.; *s.p.s.*, sutura petrosphenoidalis or sphenotympanica.

Wedged in between the massive postglenoid buttress and the massive mastoid flange, the pars petrosa and pars tympanica of the temporal bone are confined to a triangular space of limited extent. At the external apex of the triangle, the meatus acousticus externus is the predominant structure. It is not tubelike or cylindrical, but a canal between buttresses and above a thickened pars tympanica. The subparallel anterior and posterior walls of the meatus are composed of smooth bone, the dorsal roof is pitted with numerous small foramina. There is no suprameatal fossa as Segall (1943) found in Procyonidae. The ventral floor of the meatus is of an entirely different nature, being fluted along the meatal axis with longitudinal grooves and ridges. The ridges are manifested on the distal ventroexternal lip of the meatus as a series of flanges, the largest and posterior-most of which is termed herein an inframeatal spine. One has the impression that vertical plates of bone were compressed between the postglenoid and mastoid processes, in an "accordian effect," and were riddled with adventitious foramina, to give the laminated, porous appearance of the inframeatal lip. One of the grooves carries over from within the meatus around the ventral lip to the ventral surface of the bulla and dives deeply, dorsointernally, into the bone by way of a deep fossa. This fossa, the apical bullar fossa, is underlain by an apical bullar spur projecting out under it from the medial side. The entire region of the spur and fossa is perforated by adventitious foramina and indeed the fossa is probably the result of a high degree of blood vascularization in this region of the bulla.

Auditory bulla and surroundings. — The ventral surface of the auditory bulla before removal was smooth and flat. A mold and cast (SBMNH 342g) was taken of the auditory region before dissection, and a cast (USNM 23948) has also been deposited in the U.S. National Museum. The bulla was most inflated ventrally near the internal margin, about half way anteroposteriorly along the length of the bulla. From this point a very weak ridge ran to the apical bullar spur of bone projecting ventroexternally from the smooth surface of the bulla. Barely distinct shallows were aligned parallel to this ridge, fanning out anterointernally and posterointernally from the spur. The surface of the bulla was pierced by irregularly spaced small foramina, as are other areas of the basicranial surface. There was a very slight longitudinal ridge along the internal margin of the inflated bulla surface, from the region of the wall between the eustachian tube and canalis caroticus back to the posterior bullar projection.

Posterior to the apical bullar spur, wedged between the bulla and the mastoid, is a large foramen stylomastoideum widely opening ventroexternoposteriorly. In both anterior and posterior walls of the foramen can be found a smaller foramen. In this fossil, one can trace the route of the facial nerve from the region internal to the recessus epitympanicus out through the foramen stylomastoideum by means of a probe. The posteroventroexternal edge of the auditory bulla forms the floor of a distinct groove running between foramen stylomastoideum and vagina processus styloidei. Small foramina are associated with the groove, which is enclosed so well between the mastoid and bulla that it is almost a canal.

The identification and terminology of the vagina processus styloidei follows the usage of van der Klaauw (1931, p. 128): "In a few cases the hyoid lies so close against the external surface of the bulla that it forms a groove in its wall, or in the extreme condition even a canal, called the vagina processus hyoidei. Sometimes also the top of the stylohyal and the tympanostyloid cartilage is enclosed in this canal, which then is called vagina processus styloidei." He stated that Van Kampen found the tympanohyal in such a groove in juveniles of an odobenine and an otariine. Deep within the vagina in *I. downsi* is a rod-like structure that appears to be part of the hyoid apparatus, possibly the tympanohyal, fused to the wall of the bulla as in other otariids (van der Klaauw, 1931, p. 242). Thus the vagina would correctly be termed the vagina processus styloidei, as the stylohyal would lie within its confines. The ventral margin of the orificium vagina processus styloidei is a complex region, with a groove running posteroventroexternally out to the foramen stylomastoideum, a groove running posteroventrointernally, and between the two a large ventral protuberance prolonged posteriorly as a posterior bullar projection. King (1960) has emphasized a "cylindrical projection of tympanic" in *Phocarctos hookeri* that may not be a strict homologue of this posterior bullar projection. The "cylindrical projection" is continuous with the ventromedial edge of the auditory bulla (King, 1960, pl. 16) in *P. hookeri* and the comparable process in *N. cinerea* is irregularly flattened. Another, more laterally directed process in *N. cinerea* underlies the pit for the stylohyal, as does the posterior bullar projection in

I. downsi. But the specimen of *N. cinerea* illustrated by Sivertson (1954, pl. 4) does not show the lateral process so distinctly, and a perusal of the otariid basicrania illustrated by Gray (1874), particularly plates 14, 16, 17, 20, and 30, suggest to me that these structures are highly variable species to species and individual to individual, notwithstanding obvious age and sex differences. Thus the comparability of the posterior bullar projection, associated intimately with the hyoid apparatus in *I. downsi*, and the various projections discussed by King, are uncertain.

Notwithstanding its terminology and homology, the posterior bullar projection in *I. downsi* is a prominent feature of the bulla. In posterior view it is rhomboidal in cross section and the dorsal surface of the projection runs up into the vagina processus styloidei in the form of a distinct trough with discrete edges and a roughened surface. The trough is matched on the dorsal roof of the vagina by another trough extending downwards and out by means of a projecting lip, the labrum vagina processus styloidei. A canal within a canal is thus formed, leading directly to the tympanohyal far within the vagina. The distal ends of both the labrum and the posterior bullar projection are slightly pitted and rugose, as if for articulation or cartilaginous encapsulment. To recapitulate: the tympanohyal evidently lies deep within the vagina, the position of the stylohyal was evidently rigidly controlled by the posterior bullar projection ventrally and the labrum vagina processus styloidei dorsally, and yet the vagina is much wider laterally than is necessary to contain the stylohyal bone and evidently includes a separate canal internally and another externally that is in part confluent by means of an external groove with foramen stylomastoideum.

Deep within vagina processus styloidei, there is space medially around the tympanohyal, and this passageway may connect through an aperture into the middle ear cavity in the area of recessus epitympanicus. I am unable to completely prepare and probe for an aperture, but note that such a connection exists between the vagina and the auditory cavity in some living otariids. The tympanohyal is a discrete cylinder within the vagina, like a small peg appressed to the side of and within a slightly larger round hole. The vagina is so inflated that a large eminentia vagina processus styloidei is raised upon the posterior wall of the auditory cavity, running dorsoexternally from the hypotympanicum up toward the recessus epitympanicus. Such a pronounced structure in the middle ear of this extinct sea lion invites speculation as to its function.

That portion of the auditory bulla medial to the auditory cavity and ventral to canalis caroticus is perforated by a great number of foramina of varying size. As can be seen in Fig. 8, a bristle can be passed through some of the foramina. The vascularization of the ventrointernal region of the auditory bulla, adjacent to canalis caroticus, is likely correlated with a complex blood vascular system as in some living pinnipeds. Coupled with the aforementioned vascularization on the external side of the bulla, ventral to the meatus acousticus externus and intimately associated with the apical bullar fossa, it is reasonable to speculate that the auditory bulla of *I. downsi* was perforated by numerous blood vessels. Blood plexuses in the middle ear of pinnipeds have been described by Tandler (1899), Denker (1900), Gray (1905), and Odend'hal and Poulter (1966), and speculations as to the function of such plexuses in regulation of pressure during diving within the middle ear have been offered (Odend'hal and Poulter, 1966; Graham, 1967; Møhl, 1967). Without knowledge of the soft tissues in the middle ear of *I. downsi* comments as to the function of increased bullar vascularization are entirely speculatory but it is possible that the condition is associated with adaptations to diving and pressure regulation.

The back edge of the bulla in this region is rounded and forms the posteroexternal lip of the foramen caroticum posterius. The ventromedial edge is curved, sharpened into a crest, and articulates via sutura tympano-occipitalis with the basioccipital in a sutura harmonia. Viewed from the internal surface, the ventrointernal edge of the bulla is seen to be curved, and slopes ventrointernally forming a shelf. Above the shelf the medial wall of the bulla and canalis caroticus is vertical and relatively flat. The canalis caroticus opens beneath the pars petrosa, and imprints deeply the wall of the bulla. The entire external margin of foramen caroticum posterius is composed of tympanic bone, and a flange from the bulla projects over the posterodorsal region of the canal. This same flange makes up the tympanic contribution to the anteroexternal margin of the foramen lacerum posterius. A break in the external wall of the canalis caroticus discloses that the pars petrosa might have contributed to the roof of the canalis caroticus. The region is broken, but

this distinct possibility exists. The inflated, curved portion of the internal bullar wall posteriorly stops abruptly near the foramen lacerum posterius, near some canals emerging from between pars petrosa and pars tympanica. The region of these grooves, the hiatus petrotympanicus, lies in the posteroexternal wall of foramen lacerum posterius.

Anteriorly the pars tympanicus encloses or borders two major canals and forms a saddle-shaped structure. The internal canal, canalis caroticus, emerges from within the confines of the tympanic in a slightly ventral direction. Dorsal to the foramen caroticum externum the roof of the canal is incised and thus forms foramen caroticum internum. The internal carotid canal lies in a saddle-shaped structure with ventrolateral and posterior walls composed of tympanic, and a dorsoexternal wall partially composed of sphenoid. The anteroventroexternal wall, of tympanic, is pronounced into a processus styliformis (not specifically the processus styliformis of van der Klaauw, 1931, p. 133, but a general and useful term) between the canalis caroticus internus and the canalis musculotubarius. A ridge projects downward from the sphenoid to take part in formation of the wall formed by this processus styliformis. The canalis caroticus itself is ovate dorsoventrally at the foramen caroticum externum. The ventral margin of this foramen overlies one lesser and one major fossa that is perforated by numerous adventitious foramina of large caliber. The internal margin of foramen caroticum externum is broken. Canalis musculotubarius is of larger bore than canalis caroticus, but the internal portion, tuba auditiva, is about equal to the latter in size. The dorsoexternal roof of canalis musculotubarius is composed of sphenoid bone, the remainder is of tympanic bone anteriorly. The suture between the tympanic and sphenoid runs along the external wall of the canal for musculus tensor veli palatini, and 1 mm or less dorsointernally another groove parallels this suture. The groove within the auditory cavity is likely a continuation of the same groove, although I cannot probe it as it runs within the sphenoid bone between these two points.

The fragment of sphenoid bone preserved runs back well between the pars petrosa and pars squamosa and above the pars tympanica of the temporal bone, but it is difficult to trace such sutures as sutura sphenosquamosa dorsally due to preservational phenomena. The sphenoid contributes sheathing atop the canalis musculotubarius as far back as septum canalis musculotubarius within the auditory cavity, and contributes to the wall of the canalis caroticus internus. One can also identify in this fossil the posterior edge of a large foramen ovale within the sphenoid. The sutura sphenosquamosa, medial to the fossa glenoideus, runs back as the sutura petrotympanica into a second fissure behind the fissura petrotympanica containing two foramina of large caliber. I am unable to probe these foramina, hence my reluctance to identify them although one may be for exit of nervus chorda tympani. The auditory bulla does not contact the pterygoid, as in phocids (van der Klaauw, 1931, p. 113).

The dorsal or cranial face (facies encephalica) of pars petrosa bears a prominent fossa, meatus, and a number of prominent surficial features. In a medial view it can be divided into a number of regions, including: a bulbous section appressed to the pars tympanica; an overlying, flattened region containing the meatus acousticus internus; and a posterodorsal part containing the semicircular canals and cerebellar or subarcuate fossa. The ventral bulbous region is set off from the more dorsal, flattened part by a flange of bone beneath the meatus acousticus internus and an underlying sulcus. The bulbous section below this would probably contribute to the external wall of the canalis petrobasilaris, and perhaps even preclude the tympanic wall of canalis caroticus from taking part in formation of the externoventral wall of canalis petrobasilaris. In Otariini and many other otariids this medial edge of pars petrosa below meatus acousticus internus is flat and obliquely situated, or is excavated by canalis petrobasilaris, but in *I. downsi* it is bulbous and pronounced internally. Anteriorly in the region of apex pyramidalis the bulbous part is continuous with the overlying flat part, but posteriorly it flattens markedly under aqueductus cochleae. Posterior to this it roofs hiatus petrotympanicus. The division between the lower bulbous part and dorsal flattened part runs below the meatus acousticus internus, through aqueductus cochleae and slightly dorsally through the wide irregular sulcus leading into aqueductus vestibuli. Aqueductus cochleae is roofed dorsally and posteriorly by a bony trough projecting far internally into the cerebellar cavity. This region posterior to the meatus shows squared corners and vertical walls, unlike the sloping surfaces in Otariini.

The meatus acousticus internus is large, divided into a canal anteriorly for nervus facialis and one posteriorly for nervus acousticus by a low transverse crest. The meatus is altogether 6 mm wide and about 2 mm high, with a dorsal lip curving back to incompletely roof the meatus internally. The region dorsal to the meatus is flat, defined anteriorly by a continuation of the sulcus beneath the meatus, again emphasizing the resulting double nature of the surficial features of the pyramid. This dorsal region is slightly striated along its main axis, anterointernally. The canal for the trigeminal nerve is found anteroexternally. The posterior region of the pars petrosa is raised into a hollow hummock, and contains the semicircular canals. The anterior semicircular canal is oriented almost transverse to the axis of canalis musculotubarius, the crista for the posterior semicircular canal is oriented slightly anteroexternally of the same axis. The anterior semicircular canal encircles a foramen leading into the cerebellar or subarcuate fossa, the margin of the foramen is slightly irregular and bumpy, not smooth and rounded with fine, radiating striae as in many Otariini. The greatest transverse width of the foramen is 65 mm, its height 3.2 mm and the anteroposterior depth of the fossa over 9 mm. Thus the fossa is deeper than wide, unlike the Otariini and Arctocephalini in which it is shallower than wide. The fossa is divided within into two main subfossae by a longitudinal ridge on its floor, and dorsally within the fossa near the entrance, are a few longitudinal crests. Externally adjacent to the hummock containing the semicircular canals, the petrosal crest and tentorium are appressed to the hummock such that the tentorium contacts and is appressed to canalis semicircularis ossei anterior on its external side, unlike living Otariini and Arctocephalini.

Middle ear region. — As stated before, the ventral floor of the auditory bulla was dissected away after precautions were taken to illustrate and cast the specimen. Most of the structures in the middle ear were found undamaged and allowed detailed preparation. Two fragmentary ossicles, malleus and incus, were found in the epitympanic recess. Description, illustration, comparisons, and interpretation of these ossicles will be included in a comparative treatment of fossil otariid ear bones now in preparation. The cavity of the middle ear is relatively elongate and deep. It is in general confined within tympanic (=entotympanic plus ectotympanic) bone except for elements sheathing the roof of the auditory cavity like the pars petrosa and sphenoid. There are no sinuses extending into exoccipital, mastoid, or other surrounding elements. The three major regions of the auditory cavity recognized by van der Klaauw (1931, p. 19) are not well defined. Neither is there a septum bullae, nor is the auditory cavity divided by other septa. The hypotympanic sinus or hypotympanicum is expanded, particularly ventrally and posterointernally; the crista tympani projects into the auditory cavity and thus, following Bondy (1907, p. 394 cited by van der Klaauw, 1931, p. 201) the boundary between the auditory cavity and the recessus meatus is projected within the general confines of the cavity; and the primary tympanic cavity, containing principal elements such as the auditory ossicles, is small relative to the size of hypotympanicum. Part of the true tympanic cavity, the recessus epitympanicus, contains only parts of the malleus and incus (van der Klaauw, 1931, p. 73), and the remainder of the primary tympanic cavity encompasses the rest of the ossicles and associated working parts of the middle ear from the tympanic membrane to at least the fenestrae vestibuli and cochleae.

I can find no sure distinctions between possible entotympanic and ectotympanic elements. A fine line, possibly a break but also possibly a natural suture, extends from the dorsal edge of the bulla wall, behind fenestra cochleae on the posterodorsomedial wall of the auditory cavity, straight down to a point opposite the posterior bullar projection, medial to the eminentia vagina processus styloidei. It is conceivable that this line might delineate the entotympanic medially from the ectotympanic, in which case the structures associated with the hyoid arch would lie in ectotympanic bone or between the entotympanic and ectotympanic. Some evidence (papers by Van Kampen, cited by van der Klaauw, 1931, p. 283) indicates that in Otariini and Odobeninae the entotympanic–ectotympanic suture ends in the region of the vagina processus styloidei or between it and the foramen stylomastoideum, but I find in a young *O. rosmarus* skull the entotympanic–ectotympanic junction internal to the vagina a short distance (LACM M702). In a skull of *Z. californianus* (Elliot, 1904, pl. 53) a sulcus on the bulla lies internal to the vagina in the adult skull. In a fetus of *O. byronia* (Camerano, 1882?, pl. 3) the ectotympanic is ring shaped and the suture lies posterolateral on the bulla, in the region of the vagina which in this species

also lies posterolaterally. Thus the line, above mentioned, is in approximately the expected position.

The tympanic bones encompass much of the auditory cavity, and curve dorsally inward to form a little of the auditory cavity roof. The remaining open space dorsally, foramen magnum bullae, is roofed by pars petrosa, pars squamosa, and other elements. The tegman tympani of the pars petrosa enters the roof around and including the promontorium. Onlapping this element from below on posterior, medial, and anterior margins is the entotympanic and possibly part of the ectotympanic. The entotympanic–ectotympanic boundary is not distinct. An oblique axis in the middle of the roof of the auditory cavity, parallel to the external margin of the facial canal through the recessus epitympanicus, defines the medial portion of the roof, composed mainly of tegman tympani of pars petrosa, from the lateral portion, with regions such as the recessus epitympanicus being roofed dorsoexternally, presumably with pars squamosa of the temporal bone. The sphenoid sends posteriorly a sheet of bone roofing canalis musculotubarius back to within septum canalis musculotubarii. This sphenoid plate is underlapped by entotympanic bone medially in a sutura squamosa and underlapped by ectotympanic laterally in a sutura harmonia. The most posterointernal spine of the sphenoid lies between pars petrosa, ectotympanic, and possibly pars squamosa. Assuming that the foramen stylomastoideum–facial canal posteriorly lies between pars mastoidea and ectotympanic, the posterior end of the recessus epitympanicus ends at about the same level as, or only slightly posterior to, the level of the most posterodorsal bend of the facial canal as it departs the auditory cavity. I cannot prepare to completion the small crevice at the back end of the recessus epitympanicus, representing sutura petrosquamosa, but it appears as if there is no significant prolongation of the recessus into pars mastoidea, and no epitympanic sinuses developed. Sutura tympanosquamosa lies longitudinally along the external wall of recessus epitympanicus.

The septum canalis musculotubarii is a flange projecting internodorsally from the external, ectotympanic wall of the auditory cavity, underlying musculus tensor veli palatini. The anterior surface of the eminentia vagina processus styloidei is likely composed of tympanohyal bone, as that element can easily be discerned by differences in texture of bone surface. Thus the auditory cavity as a whole is bounded by contributions from: ectotympanic and entotympanic of pars tympanica; sphenoid; tympanohyal; pars petrosa, pars squamosa, and pars mastoidea of the temporal. The bulla does not contact the exoccipital or the pterygoid bone. I have not discussed the subdivisions of the sphenoid, but note that in juvenile (LACM M783, M785) and adult (M1692) skulls of *Eumetopias jubata* a suture runs from foramen ovale back, separating the sphenoid spine wedged between the pars squamosa, pars tympanica, and pars petrosa into two slips. I assume that the outer slip is a spine of the alisphenoid element, the inner, basisphenoid. Both touch the auditory bulla, notwithstanding the comment of van der Klaauw (1931, p. 117) that the basisphenoid does in odobenines but does not in Otariini.

The dorsal roof of the auditory cavity behind the promontorium is formed in part by facies tympanica of pars petrosa, underlapped posteriorly by pars tympanica. The posterodorsal-most extension of the auditory cavity, behind the fenestra cochleae, is a globous pocket set off from the remainder of the cavity to some extent, particularly by the swelling of eminentia vagina processus styloidei externally. The globous cavity is directed toward, and walled anteroexternally by, fenestra cochleae. In its posterior wall is a small foramen, opposite to the posterior bullar projection, the latter evidently being composed of solid bone. The space within the auditory cavity is not subdivided by any major septa. The foramen pneumaticum, between the primary tympanic cavity and hypotympanicum, is completely open and unconstricted.

Major structures within the auditory cavity include the bulge of the canalis caroticus, promontorium and adjacent facial canal, eminentia vagina processus styloidei, recessus epitympanicus, crista tympani, septum canalis musculotubarii, and the canalis musculotubarius. The medial wall of the auditory cavity bulges far inward, laterally, nearly touching the edge of fenestra cochleae posteriorly. The ventroposteroexternal surface of the carotid canal wall is distinctly set off from the vertical bulla wall and the anterior wall of the canal, and is slightly fluted and creased. Although broken, the bony canal wall in life may have been perforate to some degree, as the dorsal and external wall of the canal at the level of fenestra cochleae seems to have been formed

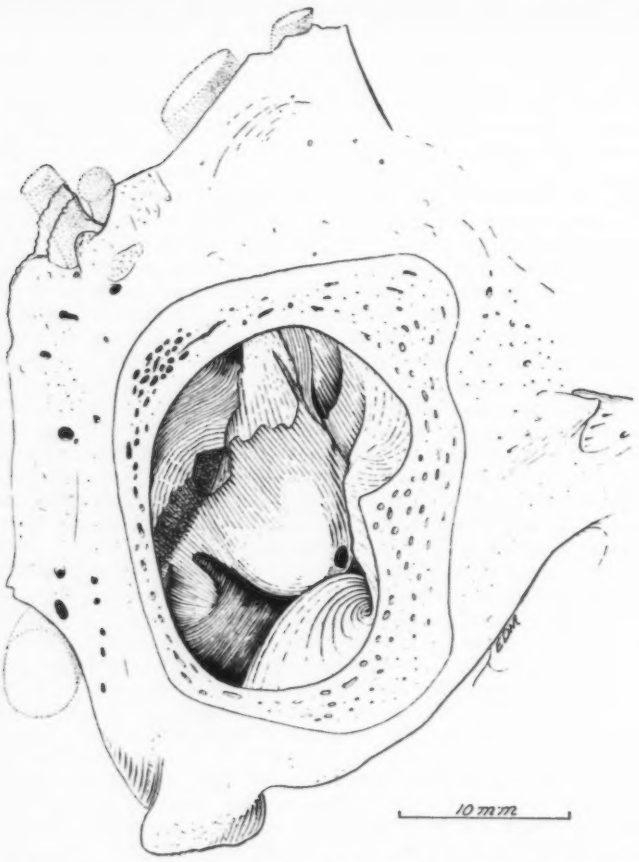

FIG. 5. Ventral view of dissection of left middle ear region and auditory bulla of holotype of *Imagotaria downsi* (SBMNH 342f) from Late Miocene or Early Pliocene Sisquoc Formation near Santa Barbara, southern California. Scale is 10 mm long.

by tegman tympani of pars petrosa, probably covered in cartilage. This lack of ossification is questionable: perhaps the exceedingly thin wall composed of tympanic has been broken away, leaving what appear to be natural edges. The medial wall of the auditory chamber wraps down around the canalis caroticus, ventrally underlies the canal almost fully, then drops vertically far below the canal to wall in an enlarged hypotympanicum. Only ventrally is the medial wall perforated by small foramina. The hypotympanicum thus underlies the canalis caroticus postero-ventrally.

The eminentia vagina processus styloidei is a conical-shaped swelling on the posterior wall of the auditory cavity, running dorsoexternoanteriorly with its apex directed dorsoexternal of the facial canal towards the recessus epitympanicus. The largely enclosed tympanohyal lies within the eminence at the level of membrana tympanica. There is thus a large groove between the eminentia and crista tympani, running dorsoexternally. A minute protuberance on the eminentia

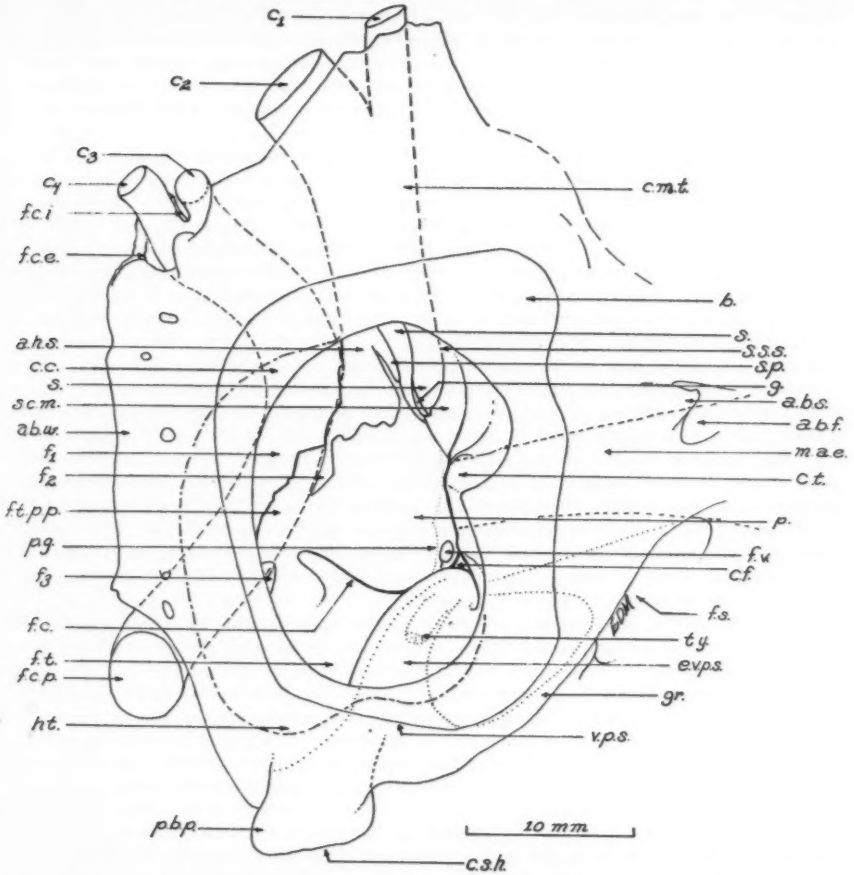

FIG. 6. Overlay of Fig. 5 giving details of middle ear structure of the holotype of *Imagotaria downsi*. Scale is 10 mm long. Abbreviations: *a.b.f.*, apical bullar fossa; *a.b.s.*, apical bullar spur; *a.b.w.*, thickened ventromedian wall of auditory bulla, perforated with numerous adventitous foramina; *a.h.s.*, anterior horizontal septum; *b.*, cut surface of the auditory bulla; c_1, schematized course of musculus tensor veli palatini and nervus tensoris tympani; c_2, schematized course of tuba auditiva; c_3, schematized course, dorsad, of arteria carotis interna; c_4, schematized course of vein from inferior petrosal sinus, and other structures; *c.c.*, schematized course of canalis caroticus defined by broken lines; *c.f.*, roof of canalis facialis; *c.m.t.*, canalis musculotubarius; *c.s.h.*, course of stylohyal from dorsal to p.b.p. to t.y.; *c.t.*, ventral lip of crista tympani; *e.v.p.s.*, eminentia vagina processus styloidei; f_1, broken ventrolateral bullar wall of canalis caroticus; f_2, fragment of lateral, bullar wall of canalis caroticus, continuous with anterior horizontal septum; f_3, fragment of posterodorsolateral bullar wall of canalis caroticus; *f.c.*, fenestra cochleae; *f.c.e.* foramen caroticum externum; *f.c.i.*, incisure in dorsal wall of canalis caroticus leading into canalis caroticum internum; *f.c.p.*, course of internal carotid nerve and artery and other structures through foramen caroticum posterius; *f.s.*, foramen stylomastoideum; *f.t.*, facies tympanica of pars petrosa; *f.t.p.p.*, facies tympanica of pars petrosa, possibly roofing portion of canalis caroticus (note that in the shaded drawing, Fig. 5, the canalis caroticus has been stippled in); *f.v.*, fenestra vestibuli; *g.*, groove in sphenoid; *gr.*, groove between v.p.s. and foramen stylomastoideum; *ht.*, posterior-most extension of hypotympanicum indicated by dot-dashed line; *m.a.e.*, course of meatus acousticus externus, indicated by broken line; *p.*, promontorium of pars petrosa; *p.b.p.*, posterior bullar projection; *p.g.*, groove across promontorium, possibly for transmission of nervus tympanicus; *s.*, sphenoid element sheathing roof of c.m.t. separated here into two slips by groove; *s.c.m.*, septum canalis musculotubarii (processus cochleariformis); *sp.*, spine composed of bone from medial wall of bulla; *s.s.s.*, sutura sphenosquamosa or sphenotympanica; *t.y.*, distal end of tympanohyal for articulation with stylohyal, within the vagina; *v.p.s.* extent of vagina processus styloidei delimited by dotted line.

almost touches the promontory. Running from the apex of the eminentia externally is a horizontal septum which passes along the dorsal margin of crista tympani and anteriorly expands to form the septum canalis musculotubarii. This septum forms the posterior, external, and anterior margins of the floor of the recessus epitympanicus, but does not form a complete floor as the recessus communicates with the remainder of the primary tympanic cavity through a large foramen about 6 mm in anteroposterior diam.

The external wall of the auditory cavity bears prominent struts that radiate anteriorly, posteriorly, and ventrally from the crista tympani. Such struts were called "rafters" in mustelids by Pocock (1921). Between the anteroventral struts are large foramina, one between each strut. The crista tympani, and thus the membrana tympanica, slopes ventrointernally well within the auditory cavity at an estimated angle of 60° from the axis of the meatus acousticus externus. Examining the crista by peering through the broken internal wall of the bulla, it can be seen nearly encircling a shallow sulcus tympanicus in which lies a fragment of a rod-like structure. This might be a remnant of an ossified ring such as I have also observed in a dissection of *E. jubata* (UCMP 67200). The crista tympani in *I. downsi* is broadly ovate, almost circular, with its longest diameter anteroposteriorly, whereas in *E. jubata* the longest diameter is more nearly vertical. The sulcus tympanicus does not completely encircle the membrana tympanica but is incomplete dorsally in the region of pars flaccida. The ventral lip of crista tympani is not as sharp edged as the remainder but is slightly more rounded off.

That portion of meatus acousticus externus adjacent to the membrana tympanica, termed recessus meatus (van der Klaauw, 1931, p. 201; Segall, 1943, fig. 10), is projected downward only slightly, has a roughened and pitted ventroexternal floor, and is not a significantly large space. The roughened floor does not seem to be a continuation of the longitudinal fluting on the ventral floor of the meatus acousticus externus. The meatus acousticus externus throughout most of its length is slightly ovate in cross section, approximately 5.0 by 6.5 mm in diam, with the long axis of the oval anteroposteriorly.

The recessus epitympanicus is a well-defined pear-shaped fossa having a dorsomedial wall of pars petrosa, a dorsolateral wall of pars squamosa, a posterior wall possibly involving pars mastoidea, and unlikely but possibly a contribution of sphenoid to the anterior wall. I cannot trace the sphenoid dorsal to and within the septum canalis musculotubarii, but I think it unlikely that the sphenoid takes part in formation of recessus epitympanicus although the tip of the sphenoid spine might reach almost to the recessus. The recessus is not inflated beyond the volume necessary to contain the auditory ossicles and encompass their movements. A distinct narrowing of the recessus posteriorly results in a region, the fossa incudis, that contains only the crus breve of the incus. Sutura petrosquamosa runs along the dorsal roof in this region. The anterodorsointernal part of the recessus is slightly expanded into an irregular fossa to receive the body and dorsal-most portion of the incus. The wall, composed of pars petrosa, between the recessus epitympanicus and the canalis facialis is slightly irregular in shape and thickness, conforming to the various excavations in the recessus for the incus. I cannot determine the structure of the anterior portion of the recessus. The anterior, external, and ventral margins surrounding the bottom of the recessus are made up of a horizontal flange, continuous across the top of the crista tympani from septum canalis musculotubarii to eminentia vagina processus styloidei. The recessus contained the bodies of the malleus and incus, but the manubrium and processus lateralis of the malleus, the processus lenticularis of the incus, and the stapes all lay without the recessus in the primary tympanic cavity.

The external wall of the auditory bulla anterior to the crista tympani is vertical, strutted, and a dorsal plate of bone curves internally from it as the septum canalis musculotubarii. This plate of bone is continuous posteriorly with the margin of the floor of the recessus epitympanicus. This septum (also called processus cochleariformis) forms a tube about 6 mm long and 3 mm in greatest width, through which passes musculus tensor tympani. It is effectively a trochlea for the muscle, positioned with its posterior end about 3 mm anterodorsal to fenestra vestibuli. By peering down the canalis musculotubarius, I can ascertain that the septum does not contact the dorsal roof of the auditory cavity but is only a thin, cylindrical shell that does not form a complete tube. Nevertheless, it is almost entirely enclosed. Associated with the septum anteriorly may be

the homologue of processus tubarius of van der Klaauw (1931, p. 132), but I have not dissected out modern specimens to determine the relationships of the bony plate, musculus tensor tympani, and musculus tensor veli palatini. It is approximately 3 mm in transverse diam and 2 mm deep anteriorly. Running from within the septum, anteriorly along the dorsoexternal wall of the canalis musculotubarius, is sutura sphenosquamosa which lies in a distinct longitudinal groove. Another groove parallels the suture medially on the surface of the sphenoid.

The canalis musculotubarius is obliquely ovate in cross section posteriorly, long axis ventrointernally. Only anteriorly, at ostium canalis musculotubarius, is there a slight septum ventrally between tuba auditiva ossea, internally, and the canal for musculus tensor veli palatini, externally. The partial septum is composed of tympanic. As stated above, the canalis musculotubarius is bordered by tympanic and sphenoid bone. The dorsal roof of the canalis is complex, being sheathed by numerous bones and incised with a number of grooves and foramina. The tympanic (?entotympanic) dorsal to canalis caroticus splays dorsoexternally against the ventral surface of tegmen tympani of pars petrosa in a sutura harmonia to cover the dorsointernal wall, reaching externally to contact the sphenoid spine and underlie it. The posteroexternal edge of this tympanic roofing element is thin, dentate, and underlays the tegmen tympani back to the promontorium. Its external margin bears an elongate, finger-like spine that points toward the crevasse between the promontorium and septum canalis musculotubarii. This plate of the entotympanic is here termed the anterior horizontal septum for convenience, and is the homologue of a horizontal septum in the same position in Arctocephalini, Otariini, and Odobeninae that is of variable position relative to the canalis musculotubarius depending on the inflation of the promontorium anteriorly. The sphenoid also is divided longitudinally into an internal spine and an external sheath: the former is directed into the above crevasse, the latter roofs the canal leading into septum canalis musculotubarii. The groove between the two sphenoid elements is continued anteriorly with the sphenoid as a minute canal.

The promontorium is a low, rounded structure, inflated only posteriorly, pendant from the pars petrosa about 3 or 4 mm into the auditory cavity. Its base is approximately triangular in shape, with one apex pointed posteriorly toward the paroccipital–mastoid ridge. The posterointernal face of the pyramidal-shaped promontorium bears a huge fenestra cochleae (or foramen rotundum), the entire orifice being about 6 mm wide and 3 mm deep. The fenestra cochleae faces posterointernally, directly back into the most dorsoposterior part of the auditory cavity. The secondary tympanic membrane would have been approximately 4.5 mm deep and if it occupied the entire internal margin would have been more than 7.0 mm wide. The membrane lay in an almost vertical plane oriented about 40° anterointernally from a transverse plane. Within the fenestra cochleae, the dorsal roof is irregular, with a fossa internally, a downhanging irregular mass medially and an excavation externally. The internal fossa lies in the region of a foramen opening into the cochlear region, the cochlear orifice of the aqueductus cochleae or perilymphatic duct, which opens posterointernally into the cranial cavity between the meatus acousticus internus and the hiatus petrotympanicus. The cochlear orifice of the aqueduct is underlain by a spatulate lip of bone.

The external face of the promontorium bears a foramen and a groove. The foramen vestibuli (or foramen ovale) for the footplate of the stapes is approximately 2.5 mm in greatest diam, has a beveled edge, such that the inner margin of the foramen is smaller than the external margin. The above measurement applies to the inner margin. The plane of the foramen vestibuli is oblique, ventrointernal, and almost parallel to the axis of the skull. The groove runs over the external face of the promontorium from the posterior edge below the fenestra vestibuli anteriorly. Below the anterior edge of fenestra vestibuli the groove is deeper, forming a shallow fossa, and ramifies, sending one distinct groove anterodorsally, and two or more shallow grooves anteroventrointernally around onto the anterior face of the promontorium. This pattern of grooves is reminiscent of the pattern of the tympanic plexus, in which the glossopharyngeal nerve, ramus tympanicus runs on the promontory ventral to fenestra cochleae and fenestra vestibuli, then ramifies into nervus petrosus superficialis minor which runs dorsoanteriorly over the top of musculus tensor tympani; the ramus tympanicus also giving off three (Miller et al., 1964, fig. 10–16, in *Canis*) nerve twigs of the plexus tympanicus which run anterodorsally over the promontorium. This pattern is evidently different in *Procyon* (Story, 1951, fig. 83) where, if I have

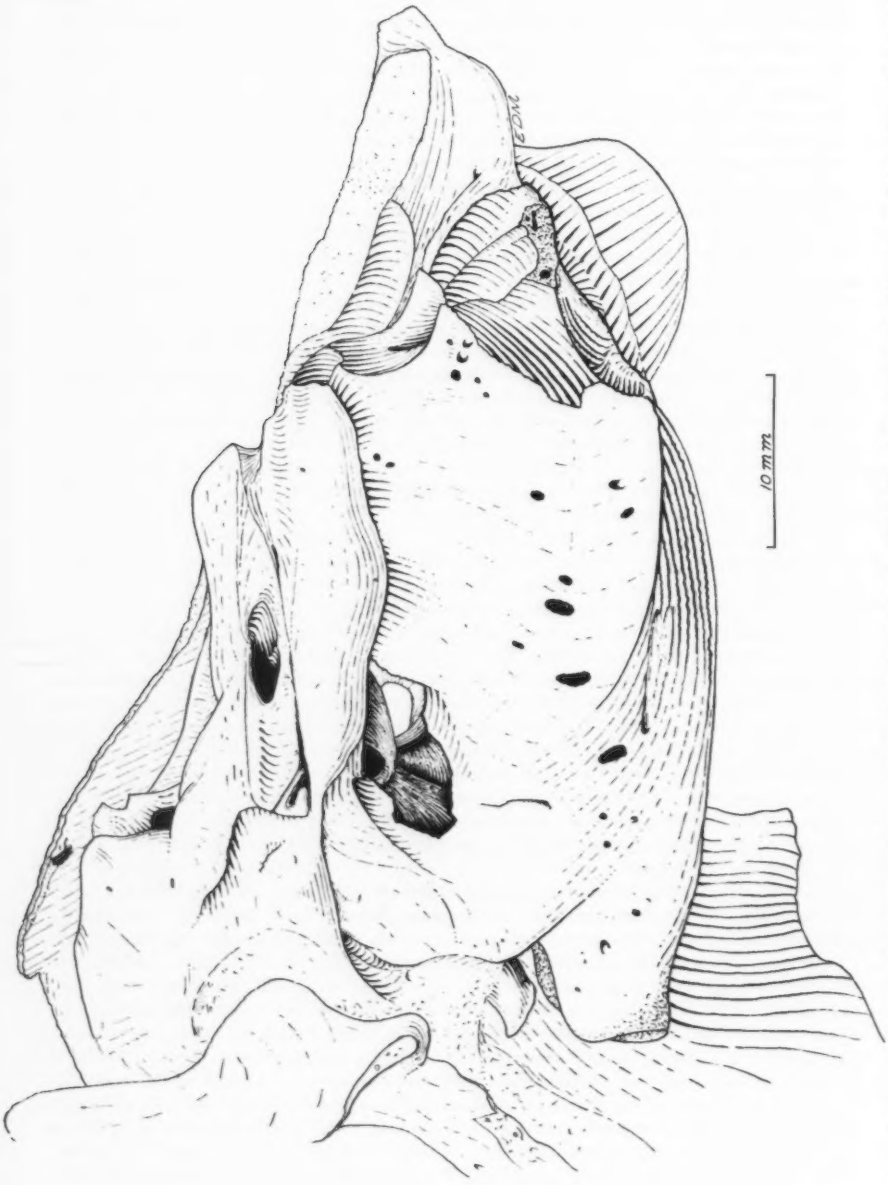

FIG. 7. Internal view of petrosal of holotype of *Imogotaria dawsoni* (SBMNH 342f) from Late Miocene or Early Pliocene Sisquoc

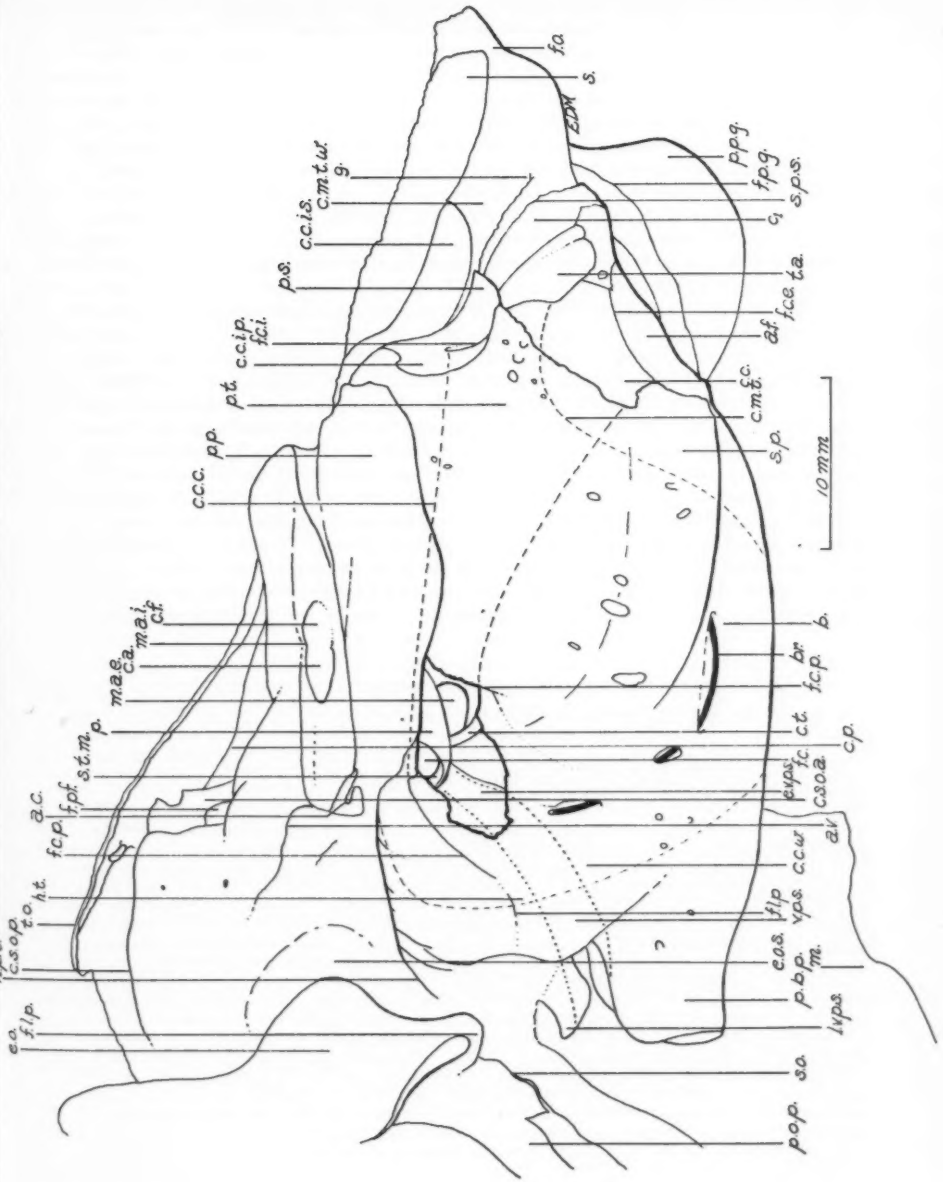

FIG. 7. Internal view of petrosal of holotype of *Imagotaria downsi* (SBMNH 342f) from Late Miocene or Early Pliocene Sisquoc Formation, Santa Barbara County, California. Scale in millimeters.

(Caption for Fig. 8 on following page)

interpreted Story's drawing correctly, the ramus tympanicus runs dorsal to fenestra cochleae instead of ventral to it as in *Canis*. It seems probable that the grooves in the promontory of *I. downsi* were associated with this plexus tympanicus and associated arteries (ramus tympanicus, arteria and nervus caroticotympanicus of Story, 1951). The nervus tympanicus enters the auditory cavity in *Canis* along the external edge of foramen lacerum posterius, but in dry specimens of otariine skulls (*Zalophus californianus*, LACM M1700; *Arctocephalus townsendi*, M1115) I find a small canal in the tympanic bone, on the external margin of foramen lacerum posterius in the wall common to the former and near the foramen caroticus posterius, that runs into the auditory cavity against the promontorium, internal to fenestra cochleae. Perhaps this canal transmits nervus tympanicus in Otariini and Arctocephalini. The canal exits into the auditory cavity in these living species between pars tympanica and pars petrosa, in a small notch in pars tympanica. In *I. downsi*, the canal probably lies anteriorly within hiatus petrotympanicus and emerges in a similar notch.

The course of the facial nerve through pars petrosa can be inferred from bony canals and grooves. As described above, the facial nerve enters pars petrosa through the anterior portion of meatus acousticus internus at an angle of approximately 57° posteroexternally from a transverse plane. It cannot be followed in this fossil until it emerges into the auditory cavity from within the pars petrosa distal to but near the geniculum nervus facialis anterior to fenestra vestibuli. Proceeding posteriorly and arching slightly dorsally in a well-defined canal, the facial nerve passes dorsal to the stapes and arches ventrally toward the end of the tympanohyal fused into the posterior wall of the auditory cavity. The facial nerve continues dorsal to the tympanohyal, still arching ventrally, and courses within and through the wall of the bulla to emerge at the foramen stylomastoideum. The facial canal from the lip of foramen stylomastoideum dorsointernally to near fenestra vestibuli is almost straight and is about 25 mm long. Near the foramen stylomastoideum, on the anteroexternal wall of the facial canal, is a small foramen, possibly for nervus chorda tympani. About half way up the canal on the posterointernal wall is another small foramen, with a longitudinal groove distally. Dorsally, up the canal still farther near

FIG. 8. Overlay of Fig. 7 giving details of petrosal structure of holotype of *Imagotaria downsi*. Scale is 10 mm long. Abbreviations: *a.c.*, aqueductus cochleae, transmitting perilymphatic duct to the subarachnoid space; *a.f.*, region of adventitious foramina; *a.v.*, aqueductus vestibuli, transmitting endolymphatic duct to the epidural space; *b.*, smooth ventral surface of auditory bulla; *br.*, bristle passed through adventitious foramina in ventrointernal bulla wall; c_1, course of musculus tensor veli palatini and nervus tensoris tympani; *c.a.*, canalis acousticus for transmission of cranial nerve VIII; *c.c.*, canalis caroticus; *c.c.c.*, course of canalis caroticus indicated by broken line; *c.c.i.p.*, wall of canalis caroticus internus comprised of petrosal bone; *c.c.i.s.*, wall of canalis caroticus internus comprised of sphenoid bone; *c.c.w.*, entotympanic wall of canalis caroticus, near foramen caroticum posterius; *c.f.*, canalis facialis or aqueductus fallopii for transmission of cranial nerve VII; *c.m.t.*, canalis musculotubarius and auditory chamber delineated by broken line; *c.m.t.w.*, dorsal wall of canalis musculotubarius formed by sphenoid bone; *c.p.*, crista petrosa; *c.s.o.a.*, canalis semicircularis ossei anterior; *c.s.o.p.*, canalis semicircularis ossei posterior; *c.t.*, crista tympani; *e.o.*, exoccipital bone; *e.o.s.*, socket in pars petrosa for articulation with exoccipital bone; *e.v.p.s.*, eminentia vagina processus styloidei; *f.c.*, fenestra cochleae; *f.c.e.*, foramen caroticum externum; *f.c.i.*, edge of foramen leading from canalis caroticus into canalis caroticus internus, adjacent to foramen caroticum internum; *f.c.p.*, lips of canalis caroticus; *f.l.p.*, margins of foramen lacerum posterius; *f.o.*, posterior lip of foramen ovale; *f.pf.*, fossa cerebellaris for paraflocculus of cerebellum, or subarcuate fossa; *f.p.g.*, foramen postglenoideum in fissura petrotympanica; *g.*, groove in roof of c.m.t.; *h.p.t.*, hiatus petrotympanicus, for passage of auricular branch of nervus vagus posteriorly, nervus tympanicus anteriorly, and other structures; *h.t.*, hypotympanicum; *l.v.p.s.*, labrum vagina processus styloidei; *m.*, mastoid; *m.a.e.*, meatus acousticus externus; *m.a.i.*, meatus acousticus internus; *p.*, promontorium of pars petrosa; *p.b.p.*, posterior bullar projection; *p.o.p.*, paroccipital process; *p.p.*, pars petrosa or pyramid of temporal bone; *p.p.g.*, processus postglenoideus; *p.s.*, a, not the, processus styliformis between c.c. and c.m.t.; *p.t.*, pars tympanicum of temporal bone; *s.*, broken edge of sphenoid bone; *s.o.*, sutura occipitomastoidea; *s.p.*, region of contact with basioccipital and basisphenoid; *s.p.s.*, sutura sphenotympanica; *s.t.m.*, groove between an osseous spiral lamina and the attachment of the secondary tympanic membrane; *t.a.*, tuba auditiva; *t.o.*, tentorium osseum; *v.p.s.*, extent of vagina processus styloidei delimited by dotted line.

where nervus facialis curves from a posterior to a ventroexternal direction, a canal of large caliber branches off from the facial canal and runs posterointernally within the bulla wall, probably between pars tympanica and pars mastoidea, to emerge as the largest and most posterior canal in hiatus petrotympanicus. The size and relationships of this canal indicate that it transmits the auricular branch of nervus vagus from the jugular ganglion in foramen lacerum posterius transversely to the facial canal where fibers of ramus auricularis join with the nervus facialis. In *Canis* (Miller et al., 1964, fig. 10–16) ramus auricularis lies anterior to vagina processus hyoidei, but in *I. downsi* and some other otariids, it lies posterior to the dorsal tip of the tympanohyal, which projects into the auditory cavity.

Since nervus petrosus superficialis major takes origin from the geniculate ganglion, and is associated with the auditory tube, its course might be associated with one of the canals in the roof of the auditory cavity between septum canalis musculotubarii and the pars petrosa. Another of the grooves might have transmitted nervus petrosus superficialis minor. The course of nervus chorda tympani can be inferred more exactly. Running within a small canal branching from within the facial canal proximal to the foramen stylomastoideum, the chorda tympani emerged into the auditory cavity through a minute foramen ventroexternal to the horizontal flange of bone running between the tympanohyal and the dorsal margin of crista tympani. The tip of this flange, slightly projected into a spur, would be the analogue of the "cartilago" of Davis and Story (1943, fig. 2) or the caudal "Chordafortsatz" of Bondy (discussed by van der Klaauw, 1931, p. 207–209), and possibly supported nervus chorda tympani. The chorda tympani probably would have crossed the ventral region of the recessus epitympanicus, between manubrium mallei and crus longum incudis, ventral to the latter, and touched the auditory wall near septum canalis musculotubarii. In man, nervus chorda tympani courses anterior to the membrana tympanica within the Glaserian fissure (Gray, 1954, fig. 954) and is transmitted through the iter chordae anterius (canal of Huguier) to the ventral surface of the skull via the fissura petrotympanica (Bast and Anson, 1949, p. 25). I cannot determine the size and shape of the Glaserian fissure in *I. downsi*, but assume that nervus chorda tympani runs anteroventrally to emerge in one of two foramina in the fissure at the junction of sphenoid, pars tympanica, and pars squamosa.

Postcranial axial skeleton. — Two small bones probably represent hyoid bones (Fig. 11). One bone (342p) might be part of the basihyoid, but alternatively could be the end of an epihyoid or some other element. Another element (342q) might be the tip of the stylohyoid or some similar hyoid bone. The interpretation of these two bones must await better comparative materials.

A partial atlas (342w, Fig. 10, 11), missing the left transverse process and most of the dorsal structures, has rather flat articular surfaces for receipt of the axis. *Allodesmus kelloggi* has similar, flat posterior facets but there are few other points of resemblance on a detailed level between the two atlases; the partial altas is much like those of most Otariini. For example, the stirrup for the odontoid process of the axis in the ventral body of the atlas (the fovea dentis) is well developed in the Lompoc atlas to much the same degree as in living Otariini, but is virtually absent as a concave facet in *A. kelloggi*. In having a distinct shelf posteroventral to this odontoid facet, a transverse foramen that faces directly back instead of posterodorsally and is bounded with a prominent ridge dorsally running out on the transverse process or wing, the Lompoc fossil is more like another Miocene fossil, LACM 591. This last is a fragment of an atlas reputedly from the "Lower Modelo," collected January 29, 1940 on the "N. side of St. Monica Mountains, S. of Tarzana." Some selected measurements of the Lompoc atlas (342w) are: across the medial lips of the transverse foramina posteriorly, about 7.8 cm, estimated; least width between foramina on ventral surface of wing, 6.0 cm; greatest width across lips of surfaces for occipital condyles, about 9.2 cm; least anteroposterior length of body of atlas, 3.6 cm.

The fragment of a vertebral centrum (342x) shows the anterior epiphysis removed or lost but the posterior one in place although not well fused to the centrum. In the vertebral column of an adult male *Z. californianus* (LACM M658) most of the anterior vertebral epiphyses are fused to some degree but most of the posterior ones are unfused or poorly fused. The fossil centrum is not significantly different from centra of thoracic vertebrae in the vicinity of T4–T5 in the *Z. californianus* skeleton, except in being of a larger size. Another fragment of bone (342y) possibly represents the tip of a neural spine or transverse process from a vertebra of unknown position.

TABLE III. Measurements in centimeters of humeri of holotype of *Imagotaria downsi* (SBMNH 342). Approximations are in parentheses.

	Right (342ad)	Left (342ac)
Length, capitulum to a line tangent to external and internal distal trochlear edges	29.8	–
Length, proximal tip of greater tuberosity to a line tangent to external and internal distal trochlear edges	31.7	–
Length, proximal tip of lesser tuberosity to a line tangent to external and internal distal trochlear edges	28.0	–
Effective (functional) length, capitulum to most proximal concavity of trochlea	28.7	–
Length of deltoid crest, greater tuberosity to distal extension of rugose muscle attachment	–	23.1
Width of deltoid crest across deltoid tuberosity (or greatest width)	2.5+	–
Greatest transverse diameter of capitulum	9.0	8.8
Anteroposterior diameter of proximal end, through capitulum and greater tuberosity	11.5	11.3
Greatest proximal diameter of lesser tuberosity	(3.5)	(3.5)
Least transverse diameter of shaft	–	4.2
Greatest width through entepicondyle and ectepicondyle	10.8	–
Greatest anteroposterior diameter of medial trochlear edge	6.9	–
Greatest anteroposterior diameter of lateral capitular edge	4.3	–
Width of trochlear surface at distal extremity	7.3	–
Most posteroventral margin of proximal capitulum to most dorsoposterior margin of distal trochlear surface	19.6	–

Two fragments (342ae and af) from the capitula of ribs, and three specimens (ag–ai) from the shafts of ribs, yield little information. The cross section of one rib fragment is nearly round with diameter of at least 1.9 cm, another fragment is likewise nearly round but shows one flattened surface.

Two fragments of bone (342u and v) are undetermined, as are two other fragments 342aj and ak.

Scapulae. — Two fragments from the glenoid region of the scapulae (342aa, right; 342ab, left) show that the glenoid fossa was up to 6.1 cm in transverse diameter and very gently concave (Fig. 11). The scapular tuberosity is small but the coracoid process is extremely large: massive and long, it projected far down over the head of the humerus. The base of the scapular spine under the acromion process was far ventral on the scapula, within 2.7 cm of the lip of the glenoid fossa. The large coracoid process is relatively the largest in any Otariini. Another fragment from one of the scapulae (342z) is not certainly identifiable but represents a border, possibly part of the caudal border.

Humeri. — Both humeri are preserved, neither complete (Fig. 12–14). The right humerus (342ad) has the ends intact but the shaft is damaged, the left (ac) is missing the distal end and a portion of the deltoid crest but shows the parts damaged on the right humerus. Thus a complete picture can be constructed of the humerus, as in the following composite description. Measurements of both humeri are presented in Table III.

The humerus is relatively more massive at the proximal end than at the distal end, with a comparatively slender shaft. The distal epiphysis is completely fused to the diapophysis, leaving no trace of a suture, but the proximal epiphysis is completely unfused. The proximal end is characterized by a very high and pointed greater tuberosity that is thin transversely and higher

than the proximal capitulum or head, a low and rounded lesser tuberosity with an internal surface that projects dorsoexternally, and a large proximal capitulum that is not wider than the transverse diameter of the entire humerus taken across the greater and lesser tuberosities. In this last feature it resembles *A. kelloggi* slightly more than living Otariini. The capitulum is relatively large, with a transverse diameter about 32% of the functional length. This figure is more similar to that in *Odobenus* than in *Eumetopias* (Mitchell, 1961, p. 7). In a proximal view, the capitulum is seen to be large, the greater tuberosity high and thin and oriented along a strict anteroposterior axis, the lesser tuberosity takes a broad origin from the humerus and is directed mainly anteriorly. The dorsal and internal surface of the lesser tuberosity is distinctly set off from the adjacent surfaces. The internal surface of the greater tuberosity is pierced by large nutrient foramina.

The deltoid crest is not inflected on the anterointernal margin and does not overhang the bicipital groove as in *Z. californianus* (LACM M658) but is similar to the crest in *O. byronia* (LACM M1611) internally. In the proximal half of the deltoid crest there is no external overhang, but near the distal end there is a slight crest developed much as in *O. byronia* but not as emphasized. It is clear that the deltoid tuberosity, seen as a distinct structure in odobenines, has been incorporated into the region of the deltoid crest near its distal end as in living otariines and *Allodesmus*. At this point, where the distal end of the deltoid crest is pronounced into a broadened area, the deltoid crest is relatively less elevated from the shaft than in *A. kelloggi* (Mitchell, 1966a, pl. 15) and *A. courseni* (Downs, 1956, fig. 3). At this point the deltoid crest in *Allodesmus* and in living otariines drops abruptly to the shaft, usually in a straight line (as observed in a side view), but in odobenines the slope from the crest to the shaft distally is more gradual (Mitchell, 1961, fig. 12). The humerus of *I. downsi* resembled the former more than the latter in this feature. In anterior view, the shaft is relatively very slender. The main axis of the humerus runs from the proximal capitulum through the shaft down to the articular surface for the capitulum of the radius. The internal portion of the distal end is canted slightly inward. The internal surface of the shaft arcs downward and inward to meet the entepicondyle: at the junction this surface is nearly in the transverse plane. In most other humeri examined (Mitchell, 1961) the incline of the dorsal surface of the entepicondyle is ventrointernally; in *I. downsi* it is internally. The entepicondyle is quite large, with well-defined muscle scars on the ventrointernal surfaces. It is more pointed dorsointernally than in some otariines, well set off from the distal articular surface and perforated posteroventrally by large nutrient foramina. The ectepicondyle does not protude notably from the level of the distal end of the bone. There is a thin ridge running proximally from the low and rounded ectepicondyle on the posteroexternal margin of the shaft, which merges into the shaft at the level that the deltoid crest merges with the shaft distally. The extreme sigmoid flexure developed in some otariine humeri (the flexure along the posterior surface of the shaft observed in lateral view) is not so marked in the humerus of *I. downsi*. The shaft is relatively straighter, as in humeri of the odobenid *Alachtherium cretsii* (Mitchell, 1961, fig. 12) and *A. kelloggi* (Mitchell, 1966a). There is a small but distinct olecranon fossa, a very less distinct coronoid fossa. The shape of the articular surface on the distal end of the humerus is very similar to that in Otariini, particularly *O. byronia* (LACM M1611), but the anteroposterior diameter of the internal edge of this surface is relatively much greater, as it is in *Allodesmus*. A nutrient foramen on the posterointernal surface of the shaft plunges into the surface of the bone toward the distal end. Breaks show thick lamellar bone and a medulla that is completely filled with porous bone.

The humerus is much like that in living Otariini, with differences due mainly to features in which it is more generalized than in living species. Particularly critical, I believe, is the large head, shape of the entepicondyle, and straightness of the shaft.

Imagotaria downsi, Referred Specimen

A skull in the United States National Museum (USNM 13487), frontally sectioned and lying in two blocks of diatomite, might represent *I. downsi* but it has not yet been prepared for detailed study. Dr R. Kellogg (*in litt.*

January 13, 1967) gave me permission to examine the skull in Washington, but not to prepare it for detailed study, hence my reluctance to make this the type specimen of the new species. The specimen was collected from a quarry in the Sisquoc Formation, the same unit whence came the holotype of *I. downsi*. According to the typewritten label, it is from "The Celite Company's No. 38 Quarry, 1100 feet west from northwest corner of northeast ¼ of section 22, Township 6 North, Range 34 West, San Bernardino Meridian, 2.6 miles south and east of Lompoc, Santa Barbara County, California. Skull removed from stratum within 45 feet from top of deposit (total thickness of diatomaceous earth 3500 feet). Collected about June 10, 1926, by McKinley Stockton, specimen shipped to Remington Kellogg on June 29, 1926." Dibblee (1950) has mapped the region of these commercially worked diatomite outcrops, and concluded that the Miocene-Pliocene boundary falls within the thick diatomite sequence of the Sisquoc Formation. He concluded that nearby sediments about 1000 ft above the bottom of the section and higher are Pliocene in age (1950, p. 44). Therefore the USNM specimen could be Early or perhaps Middle Pliocene in age.

The section runs approximately through the level of the palate, the middle of the zygomatic arch, and the top of the glenoid fossa through the paroccipital–mastoid complex, the occipital condyles, and over the basioccipital. Much bone has been lost as a consequence of the split, particularly the ventral portion of the paroccipital-mastoid projection and bone of the zygomatic arches, but distinct impressions remain. Relatively little crushing or distortion has occurred.

Palate and teeth. — Even in its unprepared state the skull can yield some critical information (Fig. 15). Major measurements are given in Table II with some comparative measurements of other specimens. The bone on the mid-palatal surface is slightly porous, pierced by numerous, tiny, evenly spaced holes. Some of the incisors and some of the teeth on the right side of the palate had dropped out before preservation and were lost. The canine-postcanine tooth rows are nearly parallel. The upper dental formula as far as can be determined is I1/-I2/-I3/-C1/-PC1/-PC2/-PC3/-PC4/-+?. Incisor one is smaller than I2/, oval in cross section (about 5 mm wide transversely) and longer than wide as judged from alveolar impressions. Incisor two is larger than I1/, anteroposteriorly ovate (crown about 7 mm wide and 10 mm long), and smaller than I3/. The mold of the crown of I2/ shows that it was distinctly chisel shaped, with no indication of a transverse groove. Incisor three is nearly round in section (estimated 16 mm diam at base of crown) and diverges markedly from posterodorsally to ventrolaterally. Upper incisor three splays outward and downward, diverging from the midline at a greater angle than does the canine. All the incisors project anteroventrally, projecting beyond the tip of the skull at the level of the alveoli. Since the more dorsal portions of the snout are buried in matrix, it is not known if a knob of bone protrudes anteriorly from the snout as in some living otariines. There are no major diastemata between the incisors, canines, and postcanines, although one of 5 mm length is present between I3/ and C1/ on the right side only. The canines were relatively small, projecting downward, forward, and a little outward not as far as or only as far as the tips of the third incisors. The impressions of the crowns clearly show that the crown of the canine was teardrop shaped, with a distinct ridge on the posterior border. Near the level of the crown, the root of the canine was about 16 mm wide transversely and a little longer than wide in section. Only the first four cheek teeth are visible in the specimen as preserved in the slab at present. The first postcanine had a large crown with a bulbous posterior shelf or cingulum. The crown was

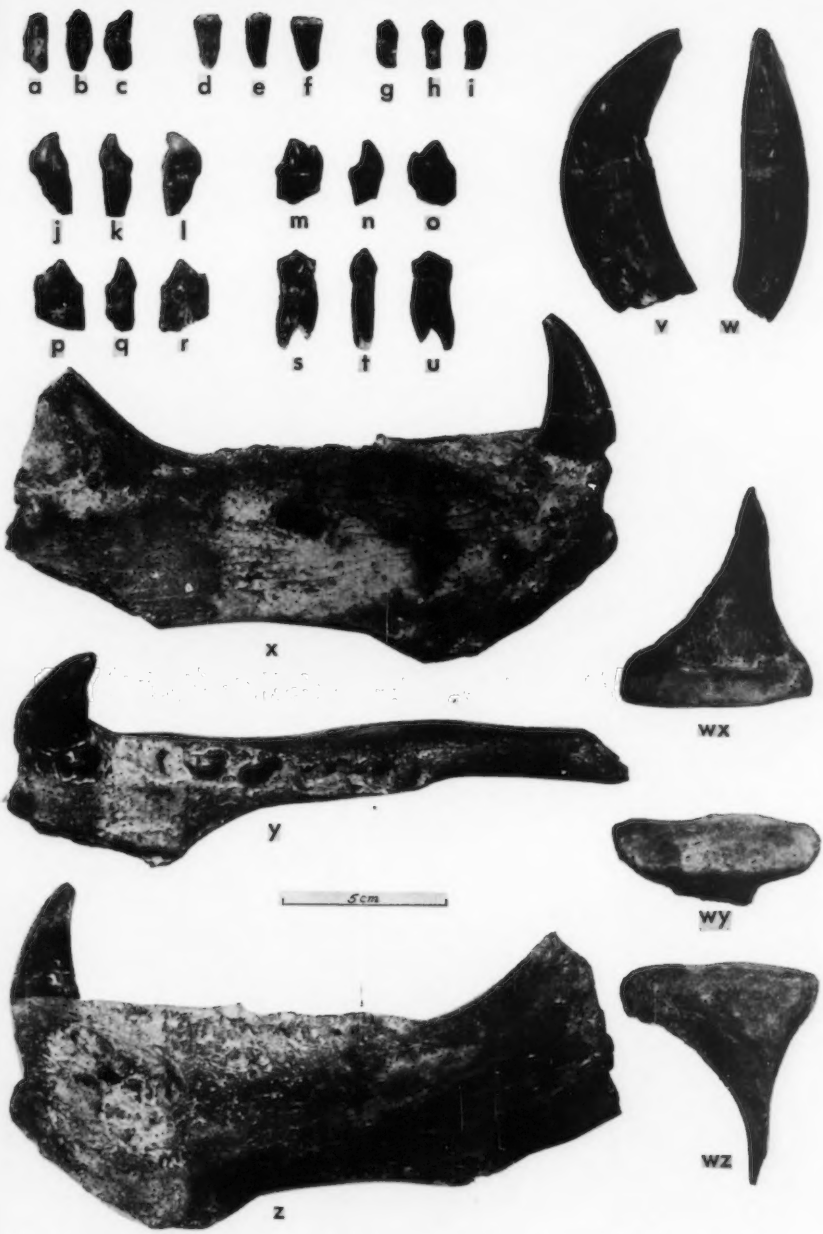

FIG. 9. Holotype of *Imagotaria downsi* new genus and species (SBMNH 342) from Late Miocene or Early Pliocene Sisquoc Formation near Santa Barbara, southern California. All views approximately one half natural size, scale is 5 cm long. Photos by Mike Hatchimonji. *a,b,c*, three views of possible lower incisor two?; *d,e,f*, three views of root of postcanine tooth; *g, h, i*, labial, anterior, and lingual views of small postcanine tooth, possibly right PC/6 (342n); *j, k, l*, labial, posterior, and lingual views of left lower postcanine two (342i); *m, n, o*, lingual, anterior and labial views of left lower postcanine three (342k); *p, q, r*, lingual, posterior, and labial views of right lower postcanine three (342j); *s, t, u*, lingual, posterior, and labial views of right lower postcanine five (342l); *v, w*, external and posterior views of left lower canine; *x, y, z*, external, dorsal, and internal views of right dentary bone; *wx, wy, wz*, dorsal, posterior, and ventral views of left mandibular condyle.

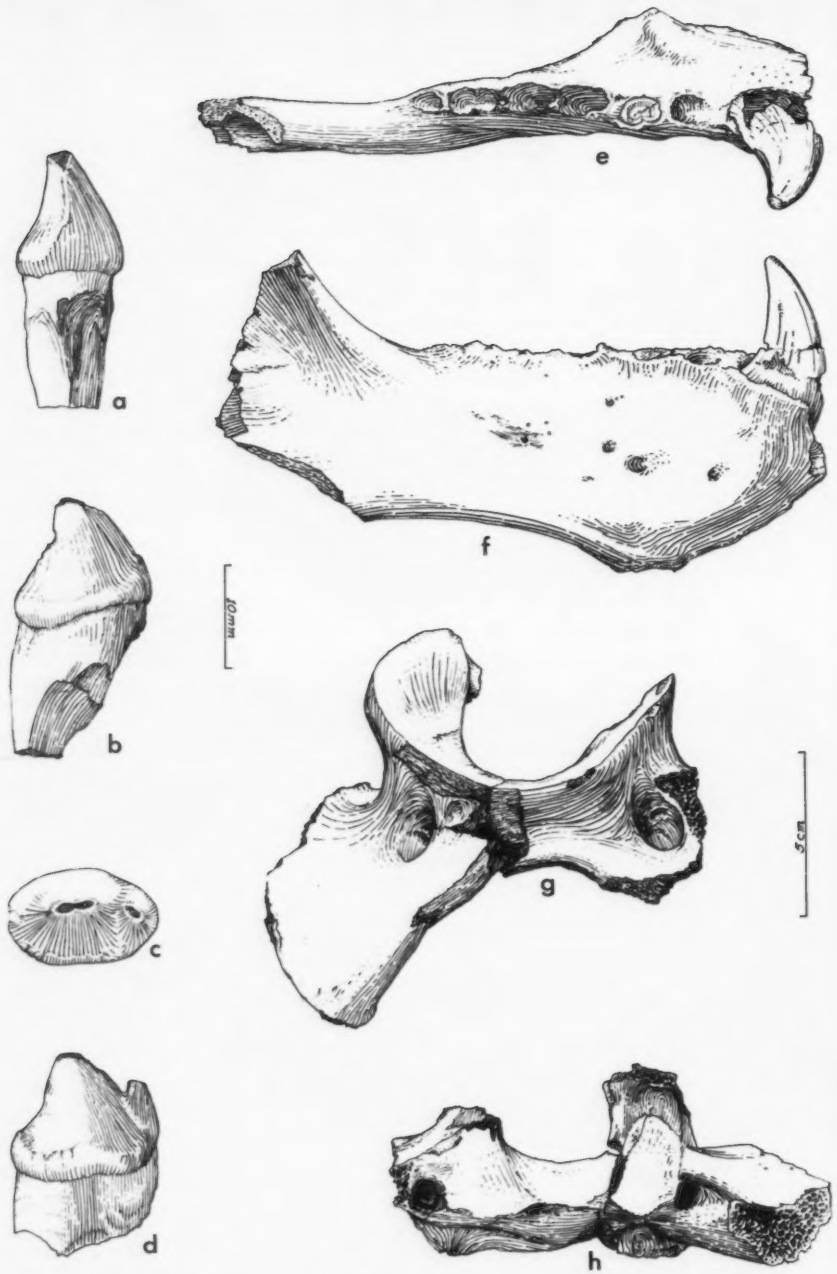

FIG. 10. Holotype of *Imagotaria downsi* new genus and species (SBMNH 342) from Late Miocene or Early Pliocene Sisquoc Formation near Santa Barbara, southern California. All views approximately one half natural size, scale is 5 cm long for jaw and vertebra, 10 cm long for isolated teeth. Orthographically projected drawings by Frank Paul. *a*, *b*, anterior and medial views of left lower postcanine two; *c*, *d*, occlusal and medial views of left lower postcanine three; *e*, *f*, occlusal and external views of right mandible; *g*, *h*, ventral and posterior views of atlas.

FIG. 11. Holotype of *Imagotaria downsi* new genus and species (SBMNH 342) from Late Miocene or Early Pliocene Sisquoc Formation near Santa Barbara, southern California. All views approximately one half natural size, scale is 5 cm long. Photos by Mike Hatchimonji. *a*, *b*, right lateral and ventral views of vertebral centrum from region of T4-T5 (342x); *c*, *d*, *e*, three views of hyoid bone (342p); *f*, posterior view of fragment from left side of lambdoid crest; *g*, *h*, medial and ventral views of glenoid fragment from left scapula (342ab); *i*, *j*, *k*, dorsal, posterior, and ventral views of atlas; *l*, *m*, *n*, medioventral, ventral, and anteroventral views of coracoid process from right scapula (342aa).

FIG. 12. Holotype of *Imagotaria downsi* new genus and species (SBMNH 342) from Late Miocene or Early Pliocene Sisquoc Formation near Santa Barbara, southern California. All views approximately one half natural size, scale is 5 cm long. Photos by Mike Hatchimonji. *a*, *b*, anterior and internal views of right humerus.

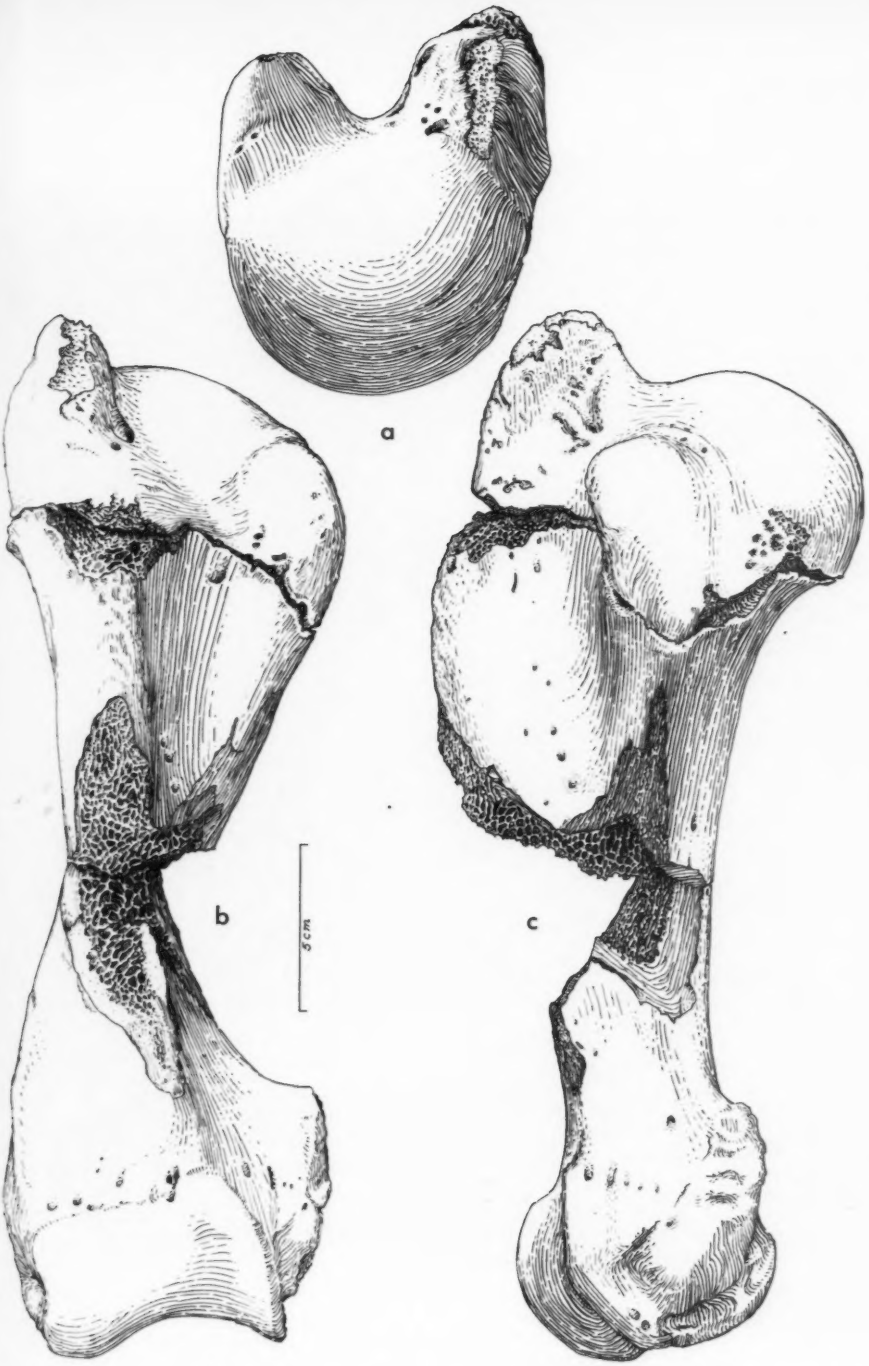

FIG. 13. Holotype of *Imagotaria downsi* new genus and species (SBMNH 342) from Late Miocene or Early Pliocene Sisquoc Formation near Santa Barbara, southern California. All views approximately one half natural size, scale is 5 cm long. Orthographically projected drawings by Frank Paul. *a*, *b*, *c*, proximal, anterior, and medial views of right humerus.

FIG. 14. Holotype of *Imagotaria downsi* new genus and species (SBMNH 342) from Late Miocene or Early Pliocene Sisquoc Formation

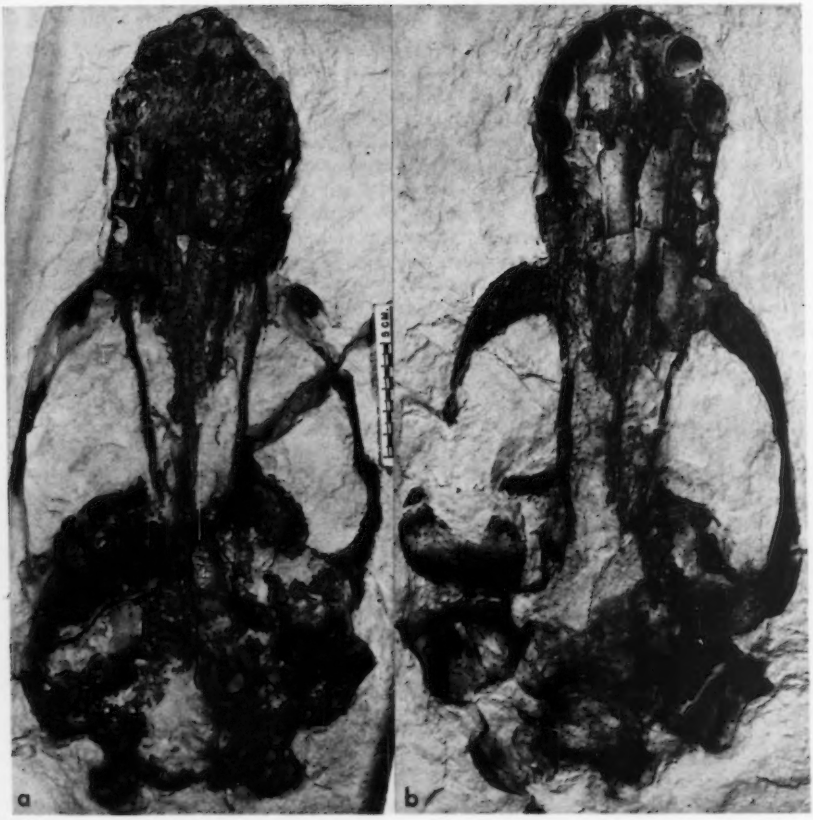

FIG. 15. Referred specimen of *Imagotaria downsi* new genus and species (USNM 13487) from Late Miocene or Early Pliocene Sisquoc Formation near Santa Barbara, southern California. Scale is 5 cm long. Photographs courtesy of USNM. *a*, *b*, reverse and obverse slabs of diatomite containing skull, sectioned horizontally.

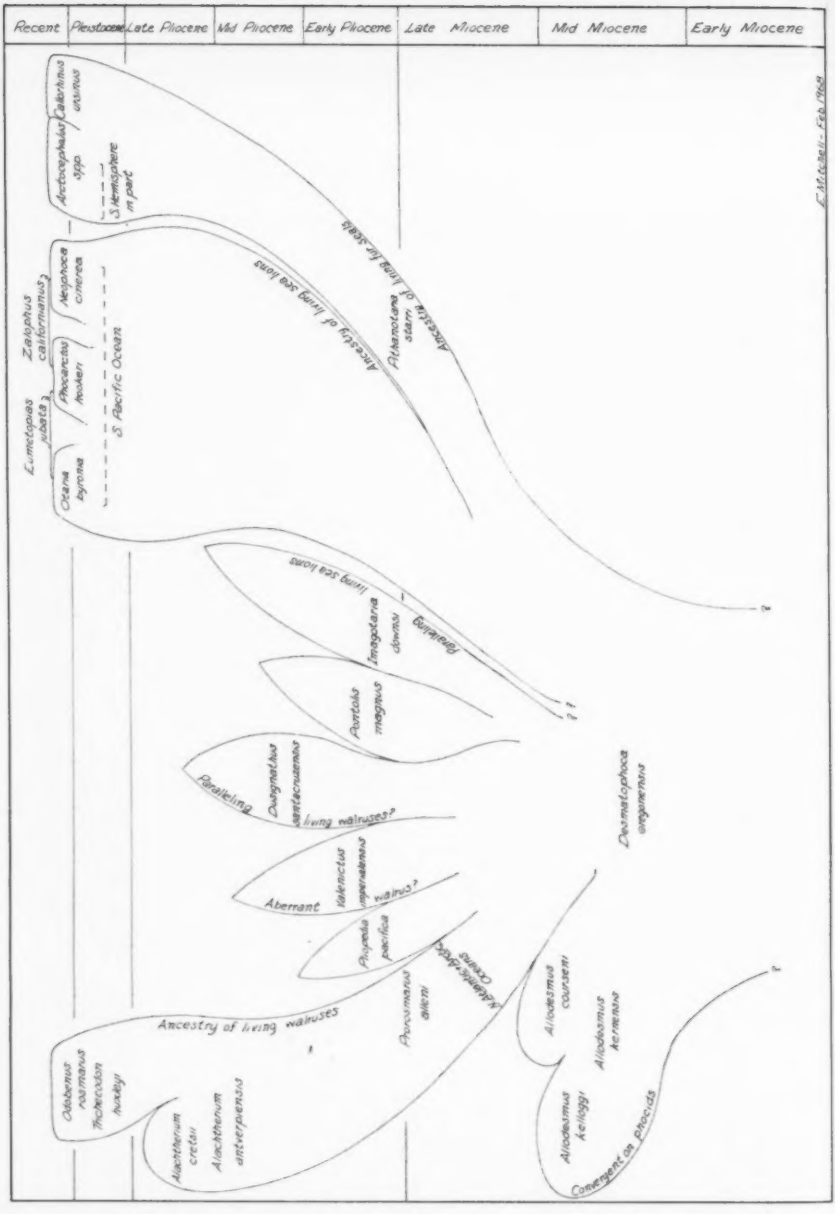

FIG. 16. Provisional interpretation of post Oligocene phylogeny of some representative North Pacific otariid species. Ordinate is time, not scaled to relative duration of epochs, abscissa reflects adaptive divergence. The omission of *Oriensarctos watasei* and *Neotherium mirum*, and other inferences, are discussed in the text. The position of *Pontolis magnus* and of *Pliopedia pacifica* is much less certain than for other species. The occurrence and affinities are shown for some North Atlantic and southern hemisphere species as well; *Odobenus rosmarus* is more Arctic than North Atlantic. The figure clearly shows that whereas only one species of the walrus lineage and only five of the sea lion lineage are extant, there has been a wide diversity of adaptive types evolved. The fur seals are presently represented by a great number of closely related species, presumably isolates resulting from a previous evolutionary burst. The late Miocene record of otariids is poor. The Pliocene species evolved from desmatophocine precursors might be grouped in alternative ways. Timing and route of entry of the North Atlantic invasion is uncertain. The ancestry of living sea lions and fur seals from a structural type such as *Desmatophoca oregonensis* is uncertain — there may have been a suitable ancestor contemporaneous with the latter species in the early or middle Miocene, making the Otariidae polyphyletic from that time.

about 15 mm long and 11 mm wide at the base, with a vertical ridge posteroexternally. The root of PC1/ may have had a slight longitudinal sulcus anteroexternally. and lay closely appressed to the root of the canine. The second postcanine had a root with a distinct longitudinal sulcus on the external side. The third postcanine is also incipiently double rooted, with a 2-mm deep sulcus on the external side only. This sulcus, seen in a cross section just above the base of the crown, divides the body of the tooth unevenly, as it lies in the forward third of the section. The alveolus for PC3/ at this level is 14 mm long and 9 mm wide. The sulcus is about 10 mm from the posterior end. The fourth postcanine evidently has two separate roots at the tip, one larger transversely oriented root posteriorly, and a smaller anterior root obliquely situated. This anterior root conforms to the orientation of the anterior lobe (observed in section) on PC2/ and PC3/, slanting from posteromedial to anterolateral. The posterior root of PC4/ lies at the anteroventral root of the zygomatic arch, its back edge 12 cm from the tip of the snout.

The snout is blunt, almost round but with an apex at the anterior margin. The incisors are therefore arranged around this curve, rather than in a straight line transversely (although this is difficult to interpret from the broken-off, slanting incisors). The snout is wider across the region of the canines than behind them, being constricted back nearly to the zygomatic arches. As is evident from the palatal impression on one slab, the palate was arched both from side to side and from front to back. There was a relatively large shelf behind I3/. An impression remains of a relatively deep pair of openings (estimated 15 mm long) into the small pair of anterior palatine or incisive foramina. Measured at the level of PC2/, I estimate the palate to have been arched to a depth of 10 mm, and perhaps even more posteriorly. On the tip of the snout, the premaxillaries were separated by a distinct suture. There is a pair of ridges or crests preserved in the cast of the palate, running symmetrically back toward the midline in the vicinity of the incisive foramina from the alveoli for I3/. If these are remnants of a premaxillary-maxillary suture, the interpretation of the teeth above would be incorrect. In this case both "I3/" and "C1/" could be canines and the skull might be that of a juvenile. However, the evidence that the skull is from an adult includes: the porosity of the palate is like that seen in aged individuals of species like *E. jubata* where the hard lamellar bone is pierced by numerous small and round holes; there are no other teeth (incisors or postcanines) obviously being replaced; the impressions of the surfaces of the occipital condyles are smooth and unpitted; and the paroccipital and mastoid processes are strongly developed. A possibility is that the animal is a juvenile with only the dual set of canines in place, the remainder of the deciduous teeth having been shed, but I think this unlikely, and that the normal dentition, with I3/, is in place. In some otariines the deciduous dentition is shed a few weeks after birth (Tomes, 1898, p. 475–476). I regard this skull as representing an adult or subadult sea lion.

A raised pair of ridges on the palatal cast represent a pair of long sulci associated with palatine foramina, and extend from the level of mid-PC2/ to beyond PC3/. The midline of the palate is well marked by a cast of a median suture or sulcus. I cannot interpret where the posterior end of the hard palate lay. The thick vertical walls of the inferior choanal tube taper back posteriorly.

Braincase and zygomatic arch. — The base of the zygomatic arch anteriorly is about 19 mm across, and the arch is much thinner (to 4 mm) and deeper at midlength. A suture between the jugal and maxillary on the dorsal surface of the arch, in the orbit, ran from the posterointernal surface to the dorsal surface of the zygomatic root just external to the infraorbital canal, and beyond. I cannot certainly ascertain the details of the jugal–squamosal junction. A fragment of the posterior end of the jugal shows that the jugal underlaps the squamosal posteriorly as far as the anterior margin of the glenoid fossa. The zygomatic arches are widest at a point nearly level with the anterior edges of the glenoid fossae.

The base of the zygomatic process of the squamosal projects laterally, roofing the glenoid fossa. The dorsal articulatory surface of the glenoid fossa slopes externoventrally at an angle of 10° from a frontal plane. The internal angle between both of these surfaces is then 160°. The glenoid fossa was bordered anteriorly by a slight preglenoid process that projected a little ventrally, and posteriorly by a postglenoid process that projected ventrally and a little anteriorly. The least distance between glenoid fossae was about 6.9 cm or about 20% of the condylobasal length.

A substantial portion of the braincase projected anterior to the glenoid fossa at about the same level or slightly higher. The anterolateral corners of the braincase were rather square. The basicranial region is only partly preserved as a cast. At the level of the middle of the bulla there is a pair of deep fossae of small diameter for the rectus capitus muscles on the basioccipital bone; the apices of these pits are 35 mm apart. The occipital condyles were large, estimated to be as much as 92 mm across.

The paroccipital, as determined from natural molds on both sides of the skull, extended all the way down the posterior end of the mastoid process and covered the posterior surface of the mastoid completely. It was less than 7 mm thick and 13 mm wide transversely, and may have been thicker near the distal end. The mastoid process is enlarged, contacting the paroccipital via a posterior ridge. The mastoid runs from the paroccipital and ends in a blunt ridge projecting ventroanteroexternally. The dorsoexternal surface of the process is smoothly curved, and the process extends appreciably below the auditory bulla. The anteroventral edge of the mastoid bears a sulcus down its middle, and the texture of the bone is roughened and irregular.

Auditory bulla. — Behind the postglenoid process are about two transverse wrinkles, in front of the bulla. The auditory bulla is relatively flat and smooth, triangular in shape, with one apex pointed posteriorly. The posterolateral margin of the bulla is sharp-edged, with a spur, 5 mm long, about halfway along it, directed ventrally and posteroexternally. The posterointernal side of the auditory bulla also had a smooth and sharp edge which hangs down about 6 mm under the basioccipital bone. A shelf of bone at the anterointernal apex of the triangular bulla projects under the eustachian canal. The combined width across the eustachian canal and the carotid canal is approximately 1.3 mm. The ventral surface of the bulla shows at least one sulcus running from the posterior apex anterolaterally, paralleling the external edge of the bulla. At least one small prominence is raised medial to this sulcus, but the bulla is relatively smooth. Enough fragments remain in the bulla region to convince me that accessory pits and spurs occurred on the ventral surface in the region of the external apex of the triangular-shaped bulla.

Referral. — In comparison with the Santa Barbara specimen (SBMNH 342), this USNM skull is similar in all critical details. Some features include: three upper incisors, progressively larger externally; I2/ has a chisel-shaped crown and is not grooved transversely; I3/ is large compared with the canine; roots of postcanines with distinct sulcus on external side, incipiently or completely double rooted; posterior root of postcanines transversely and anterior root obliquely oriented in section; palate arched from side to side and front to back; glenoid fossae surfaces slope ventrolaterally 10° from horizontal; paroccipital and mastoid processes continuous; paroccipital relatively thin lamina of bone on posterior edge of mastoid process; auditory bulla smooth, triangular in shape, with sharp and elevated external edge. In all characters comparable with the SBMNH skull save the relative size of the canine and some aspects of PC1/ and the incisors the USNM skull is alike. Canine size relative to I3/ size, as indicated above, might be related to difference not in kind but in age or sex. I refer the skull (USNM 13487) to the species *I. downsi*.

DISTRIBUTION

The holotype of *I. downsi* is from "a quarry of the Great Lakes Carbon Co. at Lompoc, California," in the Sisquoc Formation. During World War II the Dicalite Division of the Great Lakes Carbon Corporation opened a deposit east of Lompoc (Wright et al., 1954, p. 73), a completely different quarry than that from which the referred specimen came. The latter specimen is from the "Celite Company's No. 38 Quarry," the Celite Products Company having been acquired by the Johns-Manville Products Corporation in 1928 (Wright et al., 1954, p. 73). Although two different quarries are involved, they are just a few miles apart. The Dicalite Division of the Great Lakes Carbon Corporation has worked in a large diatomite deposit about 7 miles

southeast of Lompoc, on a portion of Rancho San Julian (Dibblee, 1950, p. 78), whereas the "Celite Company's No. 38 Quarry" is 2.6 miles southeast of Lompoc. Dibblee (1950, p. 78) assigned the diatomites in both quarries to the lower Sisquoc Formation. Thus the holotype and referred specimen of *I. downsi* probably came from within 5 miles of each other geographically, from the same stratigraphic unit.

Kellogg (1925a) described the distal end of a tibia and four partial ribs of an "otarid (?), new genus and species," found in 1920 near Quarry 9 of the Celite Products Company, about 1.5 miles southeast of Lompoc. The tibial fragment Kellogg likened to that of *Odobenus* of all Otariini and Odobeninae. It is possible that these bones are from an individual of *I. downsi* although I do not now refer them to that species: additional fossils are needed to confirm my guess. Odobenine-like features in the postcranial skeleton of otariids are less indicative of close relationship to *O. rosmarus* than to retention of a generalized and primitive pattern of construction. It is my belief that postcranially, *Odobenus* represents a generalized otariid (Mitchell, 1966a, p. 39), thus it is not surprising to find that such bones as the humerus of *I. downsi* show characters that might in some ways be considered odobenine. Another otariid pinniped is known from the diatomites near Lompoc, the arctocephaline *Pithanotaria starri* Kellogg (1925a). Kellogg's painstaking descriptions suggest that *P. starri* is a species of Arctocephalini, and is distinct from the larger otariid found in the same diatomites. There can be little doubt that *P. starri* does not represent a juvenile of *I. downsi.*

Some isolated teeth thought by O. P. Hay and R. Kellogg to be from *Allodesmus kernensis* were mentioned by Hanna (1923, p. 65; pl. 9, fig. *h*, *j*, and *k*). The exact stratigraphic occurrence of these teeth is unknown to me but they are evidently from diatomites at Lomita, most likely in the Valmonte diatomite member of the Monterey Shale. The teeth as illustrated look particularly undiagnostic, but one, fig. *j*, is a cheektooth with a major vertical crease down the outside of the root, with a large crown and an enlarged cingular cusp, features together found in *I. downsi* but not in *A. kernensis* or *A. kelloggi*. Thus the tooth illustrated by Hanna indicates that in the Late Miocene some species of *Imagotaria* or a related genus might have existed. This indication is confirmed when it is demonstrated below that a large sea lion skeleton referred by Lyon (1941) to *Pontolis magnus* represents in fact a species related to *I. downsi*. Yet a third specimen is known to me from the Valmonte Diatomite, this a badly distorted palate of a large sea lion with teeth incipiently or patently double rooted, enlarged lingual cingular cusps and with other resemblances to the teeth of *I. downsi*. I am attempting to track down additional data on this distorted snout, LACM specimen 17588, collected or received February 18, 1954 by Theodore Downs at the Los Angeles County Museum "from Dyrsmid from Valmonte Formation." It seems that this snout and the Lyon (1941) skeleton represent the same species.

The top of the Valmonte Diatomite Member in the Palos Verdes Hills lies below the base of the Delmontian Stage which is placed at the base of

the overlying Malaga Mudstone Member of the Monterey Formation (Bramlette, 1946, pl. 2). The lower part of the Sisquoc Formation is generally considered Delmontian, the remainder, early or even middle Pliocene. Thus by any account the fossil sea lions from Lomita are older than those from the diatomites in the region of Lompoc.

A squamosal bone mentioned below from Doheny Beach State Park came from rocks of the Capistrano Formation, which is upper Mohnian–Delmontian in age, and thus might be comparable in age to the bones from the Lomita quarry. The Doheny squamosal resembles the squamosal of *P. magnus* in many particulars, and also the squamosal of the specimen described by Lyon (1941).

COMPARISON WITH LIVING OTARIINI

On the basis of information from the holotype and from the referred specimen of *I. downsi*, I find that the most meaningful comparisons to be made are those with Otariini from the southern hemisphere. Features such as a posterior bullar projection, major lingual cingular cusps, deeply arched palate, and a high and sharp lambdoid crest are also found in *O. byronia*, *P. hookeri* and *N. cinerea*. Comments are presented in the following order: a discussion of some new specimens of *Phocarctos*; and a comparison of the middle ear of *I. downsi* with those Otariini for which I have dissected, dry skulls available.

New specimens of Phocarctos. — Sivertsen (1954), Scheffer (1958), and Mitchell (1966a) did not recognize *Phocarctos* as a distinct genus. However, King (1960) presented evidence, based upon a comparison of seven *N. cinerea* and nine *P. hookeri* skulls, that these two species deserve generic distinction. That the two populations are distinct is not in question, but as King has stated, it is not easy to decide if they are different on a specific or generic level. With a series of eight new skulls of *P. hookeri* available to me for study through the courtesy of Dr D. Johnson, I recognize that there are major differences between this species and *Z. californianus* such that *P. hookeri* cannot be included in the genus *Zalophus*, as King (1960) correctly pointed out. The skulls were collected as beach pick-ups on Snares Island, and on Enderby Island, off the northeast end of Auckland Island and on Rose Island, Auckland Island Group, in the western South Pacific in January of 1964 by D. F. Squires. My identifications below as to sex are at best a guess and subject to correction. Measurements of the eight skulls are presented in Table IV. In one of the three presumed male skulls, the nasals extend farther back than do the maxillaries. The "cylindrical" extension of the auditory bulla (King, 1960) extends posteriorly in those individuals in which it is round or ovate in cross section (mostly females?) but ventroposteriorly in those individuals (presumed to be adult males) in which it is crescentic in cross section. In the latter, there are only slight differences between the condition in *P. hookeri* and in males of *O. byronia*, in which the process is directed more ventrally and is continuous with projections on the ventro-internal edge of the entire bulla. The posterior "cylindrical projection of tympanic" of King (1960) is ventral, internal, and posterior to the stylomastoid foramen, and intimately associated with the hyoid apparatus. An extra button-like, ovate bone fused to the tip of the mastoid (ossiculum mastoideum; King and Cave, 1964) is clearly seen in *P. hookeri* skulls (male USNM 344980, females USNM 344983 and 344984-85 and others). In one specimen (344985 male?) PC2/, PC5/, and PC6/ are preserved, and PC5/–PC6/ both show distinct anterior and posterior accessory cusps. PC5/ and PC6/ are double rooted. In most of the skulls, there is a suggestion of a PC2/-PC3/ diastema, generally not found in other otariids. This is variable even in this series, however, and often where a PC2/-PC3/ diastema is found other similar diastema occur in the same tooth row behind PC3/.

TABLE IV. Cranial measurements of eight skulls of *Phocarctos hookeri*. Numbered measurements are after Sivertsen (1954); abbreviations: C, crescentic; R, round; O, ovate; D, discoid.

	USNM 344980	USNM 344981	USNM 344982	USNM 344983	USNM 344984	USNM 344985	USNM 344986	USNM 344987
Skull length, condylobasal (0)	32.5	32.2	31.4	27.3	–	30.6	25.2	–
Width of anterior nares (3)	3.5	4.1	3.5	3.0	–	3.3	3.0	–
Width across preorbital processes (5)	9.8	11.1	9.2+	7.5	7.5	8.6+	–	–
Least interorbital constriction, anterior to supraorbital processes (6)	5.4	6.3	5.3	3.8	4.2	4.9	4.1	2.6
Breadth at supraorbital processes (7)	9.0	10.2	7.5+	6.1	6.0	7.2	5.3+	4.0
Occipital crest to mastoid (point to point) (9)	14.2	14.0	13.0	10.4	10.4	12.2	10.0	7.9
Most anterior edge of palatal notch to posterior edge of incisor 1 (10)	15.0	16.2	15.4	12.8	–	14.2	11.9	–
Breadth of skull at canines (12)	–	8.7	7.1+	5.2	5.4	6.8	5.4	–
Gnathion to posterior end of maxilla (mx flange) (13)	14.9	15.0	14.8	12.2	–	14.1	11.2	–
Zygomatic breadth (17)	18.2	19.8	17.3	13.7	14.2	16.7	13.8	10.0
Breadth at mastoid (20)	16.3	16.9	14.5	12.0	12.3	14.6	11.3	8.8
Gnathion to preorbital process (point to point) (24)	11.4	12.1	11.5+	9.6	–	10.9	8.7	–
Posterior bullar projection — shape in cross section	C	C	R	R	R	O-R	D	D
Total length of nasals	6.9	7.3	7.2	–	–	6.6	–	–
Greatest anterior width of nasals	3.4	3.6	3.3	–	–	3.4	–	–
Depth of palatal concavity, measured from internal alveolar edges to dorsal-most arch of palate	1.8	2.5	1.6	1.2	1.2	1.5	1.1	–
Tooth formula (same on both sides unless otherwise indicated)	3-1-6 / 2-1-5	3-1-6 / ?-?-?	3-1-6 / ?-?-?	3-1-6 / ?-?-?	?-1-5(6) / ?-?-?	3-1-6 / 2-1-5	3-1-5(6) / ?-?-?	?-1-6 / 2-1-5

The USNM series of *P. hookeri* can be distinguished from *O. byronia* as the supraorbital process is triangular and the posterior margins of the palate are not projected ventrally. But Sivertsen (1954, p. 25) characterized *O. byronia* as having a highly arched palate with up to 35–40 mm relief, whereas the palate in other Otariinae is not arched more than 10 mm at most. On the contrary, the palate of *P. hookeri* is highly arched, its highest point being 11–25 mm above the level of the internal margins of the postcanine alveoli at any one place. Clearly *P. hookeri* is exceptional and resembles *O. byronia* in having an arched palate, at least anteriorly. It has a more generalized palate than *O. byronia*. It is deep anteriorly like that in *O. byronia* but flattened like that in *E. jubata* and *N. cinerea* posteriorly. The scars for the rectus capitus muscles are alike in *P. hookeri* and *O. byronia* in adult males, possibly more pronounced than in *E. jubata*. The "cylindrical projection of tympanic," is duplicated to varying degrees in aged males of *O. byronia* (where it is subquadrate in cross section and projects far posteroventrally) and *E. jubata* (where it is more ovate in cross section and projects posteriorly). In many of the features in which *P. hookeri* differs from *N. cinerea*, it approaches *O. byronia* (e.g. six upper postcanines, concave palate, postorbital process of zygomatic present, elongate projection posteriorly or posteroventrally from bulla).

I can only conclude that *P. hookeri* is one of the most, if not the most, generalized species of Otariini extant in the possession of: low, flat auditory bullae; long and narrow interorbital region; triangular rather than quadrate supraorbital processes; three upper incisors and six upper cheek teeth on each side; strong paroccipital process and mastoid process connected by a weak, sharp ridge; and relatively thick paroccipital process. Some specialized characters include the down and outward slope of the mandibular condyle surfaces; high arching of the palate; and posterior cylindrical projection of auditory bulla. I suggest that *P. hookeri* is a species of Otariini most closely related to *O. byronia* on the one hand and to *N. cinerea* on the other (it has been confused with the latter because of the many similarities).

Davies (1958) held that the otariids originated in the Arctic basin in common with phocids, but McLaren (1960) emphasized that the North Pacific is a reasonable place for otariid origin. Davies (1958) has hypothecated that otariids spread along an east Pacific cold-water route into the southern hemisphere by the end of the Miocene or the Pliocene, and that *Otaria* is related to *Eumetopias* in the north, and *Neophoca* to the northern *Zalophus*. It would then follow that the putative ancestor of *Eumetopias*, *P. magnus*, is the best ancestor for some southern sea lions.

It is my contention that *Otaria* may be more closely related to *P. hookeri* than to *E. jubata*, and that present evidence is sufficient to place southern hemisphere otariines in the proper context of origin from the North Pacific, but removed from *P. magnus*.

Comparison of Imagotaria downsi with skull of Phocarctos hookeri and other Otariini. — Comparison of the palate of *I. downsi* (SBMNH 342) with the *P. hookeri* series in the USNM shows similarities in: the degree of palatal arching anteriorly and palatal flattening posteriorly; and in the shape of the palatal notch posteriorly. They differ in that in the fossil: the palatines do not reach as far as the middle of PC5/ but only to PC6/ (estimated); there is a major C1/-I3/ diastema reflecting the orientation of the lower canine or a longer precanine rostrum; PC2/ (for example) has a large lingual cingular cusp not found in *P. hookeri*; the palatines are shorter and wider on the palate; the incisive foramina open up into the nasal chamber much farther back; the distance from the tip of the snout to the dorsal opening of the incisive foramina is greater than the breadth of the palate between PC1/ or PC2/; and there is more of a rostral platform dorsally.

Comparison of the temporal bone and auditory region (SBMNH 342f) with the USNM series of *P. hookeri* shows that they are similar in having a glenoid fossa that slopes dorsointernally; a spur of bone round to ovate in section, projecting posteriorly from the auditory bulla; and a bulla that is relatively flat. They differ in that in the fossil the paroccipital contributed less to the back end of the mastoid flange; there is an apical bullar spur and fossa; there is an externally directed spur of bone in the external auditory meatus on the posterodorsal edge of the ventral meatal floor; the distance between the mastoid and postglenoid process is relatively greater; the posterointernal wall of the carotid canal was formed by a flange of the basioccipital as in *C. ursinus* (USNM 11734) and not by the bulla as in most or all otariines; there is a relatively

flat surface between the anterior end of the mastoid and the paroccipital on the dorsoexternal side; a small series of foramina and a horizontal groove on the dorsal wall of the meatal tube is not developed into a major incisure or pit as in some specimens of *P. hookeri*; there is a distinct postglenoid foramen in a postglenoid sulcus or fissura petrotympanica; and the posterior lacerate foramen did not extend very far external of the level of the carotid canal, certainly not external as far as the posterior spur on the auditory bulla.

The mandible of *I. downsi* (SBMNH 342t) differs from two mandibles of *P. hookeri* (USNM 344980 and 344985) in that the fossil jaw has a sixth postcanine tooth; a distinct median ridge on the chin; a longer chin region with a straight profile of the anterior edge; ventral margin of the ramus, behind the genial protuberance, that arches dorsally rather than bellying ventrally below PC/4–PC/5; a masseteric fossa with less distinct anterior limits; a distinct fossa below PC/4–PC/5 on the external surface of the ramus; only three large mental foramina; a symphyseal surface subquadrate in shape rather than tear-drop shaped; a longer symphysis dorsally; the root of I/1 far behind root of I/2 instead of posteromedial; and more of a space between C/1 and PC/1. The fossil mandible (SBMNH 342t) is similar to two mandibles of *O. byronia* (USNM 172788 and 23240) in having a ventral border that arches dorsally behind the genial tuberosity; a straight, sloping anterior symphyseal margin pronounced into a slight ridge; a subquadrate-shaped symphysis. The *O. byronia* mandibles differ from the fossil in having a well-defined masseteric fossa that reaches almost to PC/5; a thinner ridge running up behind the teeth onto the coronoid process; only five postcanine teeth; and a short symphysis dorsally.

The generalized nature of the paroccipital relationship to the mastoid, connected by a weak, thin ridge, and the absence of lingual cingular cusps with an emphasis on anterior and posterior accessory cusps alone are enough to preclude *P. hookeri* from consideration as a descendent of *I. downsi*. *Phocarctos hookeri* and *O. byronia*, which also show similar squamosal and bulla features, are related to *I. downsi* only through a common, early ancestor.

Comparison of Imagotaria downsi and Otariini ear regions. — This discussion is based upon examination of the auditory bulla and associated structures of the following specimens: *E. jubata*, LACM M1692, M783, M785 and UCMP 67200; *Z. californianus*, LACM M419, M1734, and BM(NH) 1903.10.11.1; *O. byronia*, LACM M1715, BM(NH) 1959.12.4.6.; and upon examination of a number of illustrations of the basicranial region of Otariini (e.g. Gray, 1874; Murie, 1874; and others).

If the posterior "cylindrical projection of tympanic" in *P. hookeri* (King, 1960) is the homologue of the posterior bullar projection of *I. downsi*, it would serve to stress the similarities between the two species and separate them from other Otariini to a degree. *Phocarctos hookeri* has in some individuals almost no trace of a vagina processus hyoidei (specimen BM(NH) 1851.7.18.48, young male). It is developed to its highest degree, as vagina processus styloidei, in *I. downsi*, particularly in being inflated into the auditory cavity as an eminence. It is present, deep, and slightly inflated in *Z. californianus*, *E. jubata*, and *O. byronia* as well, situated well to the rear of the foramen stylomastoideum, and divided from it by a massive bony septum, a fusion of mastoid and bulla. (The "auricular" foramen of Murie, 1874, pl. 76, fig. 6, between meatus acousticus externus and the "stylo-mastoid" foramen, is incorrect: the former is foramen stylomastoideum, the latter vagina processus styloidei.) The vagina in *O. byronia* is even more pronounced, as the "cylindrical projection of tympanic" encloses it anteriorly and internally forming a large fossa. The vagina possibly opens into the auditory cavity, indirectly, in *I. downsi*, but I have probed the through connection in many specimens of extant otariids. It is almost blind in one adult male *Z. californianus* (M419), but broadly open in an old adult and a young female *E. jubata*. In the one undissected skull of *N. cinerea* available to me (BM(NH) 1925.10.8.32) it appears to be almost blind as in *Z. californianus*. The position of the surficial orifice of the vagina varies slightly, being directly behind the bulla in *I. downsi*, and generally posteroexternal to the bulla in Otariini. The distinctness of associated structures such as tympanohyal within the vagina, the dorsal lip, and ventral lip (posterior bullar projection), taken together distinguish *I. downsi* from all other otariids. In *E. jubata* (LACM M785) sutura entotympanica–ectotympanica lies along the internal wall of the vagina.

In *I. downsi* there is an apical bullar spur and apical bullar fossa not appreciably present as a distinct structure in any otariine. In this region in Otariini there is often a sulcus and associated vascularization of the bone surface, but no distinct spur or fossa. The inframeatal flanges and processes are, however, found in all otariids to a variable degree. In most Otariini the auditory bulla is ventrally inflated to some degree immediately behind the glenoid fossa and is emphasized anteriorly even to the point of entering the glenoid fossa as an accessory flange medial to the postglenoid process. This flange is most pronounced in *Z. californianus* and *E. jubata*, least so in *O. byronia* and *I. downsi*. The postglenoid foramen is relatively larger in *I. downsi* than in Otariini. The septum canalis musculotubarii is fully developed in *I. downsi*, but markedly reduced or absent in Otariini. The membrana tympanica of *I. downsi* lay with its longest diameter in the horizontal plane or was almost circular, but in living Otariini the largest diameter is often distinctly in a vertical plane and the membrane is definitely elongate, and ovate in shape. The anterior horizontal septum is closely appressed to the roof of the auditory cavity and canalis musculotubarius in *I. downsi*, and the promontorium in this region is not inflated. In Otariini, the anterior horizontal septum does not strictly roof the canalis musculotubarius but is intermediate (*E. jubata*) or evidently floors the canal (*Z. californianus*). In no Otariini does it bear such a distinct, finger-like process on its external edge, as in *I. downsi*. The canalis caroticus bulges far into the auditory cavity in *I. downsi*, perhaps more so than in Otariini. The globous space posterior to fenestra cochleae is similar in *I. downsi* and *E. jubata*, in which the space is enlarged, walled completely and tightly up to pars petrosa by tympanic sheathing. The sheathing does not tightly appress to pars petrosa in *O. byronia*, and the space is of different shape, more elongate and more ventrally situated in the wall of the tympanic in *Z. californianus*. Fenestra cochleae is very large in *I. downsi*, with its greatest diameter transversely situated. This is also the case in *E. jubata* and in *O. byronia*, but in *Z. californianus* the long diameter is more nearly vertical. There is no great vertical flange below crista tympani in *I. downsi*, but its presence seems to be variable in *E. jubata* and *Z. californianus*. The epitympanic recess in Otariini seems not to be inflated over the size found in *I. downsi*.

The dorsal face of pars petrosa bears a blind fossa in Otariini that is usually not as deep as wide, but in *I. downsi* this subarcuate fossa or fossa cerebellaris, for the paraflocculus of the cerebellum, is bipartite, relatively more excavated and spacious within, and is deeper than the transverse width of its entrance. Although this region is the starting point for resorption of the canalicular capsule (Bast and Anson, 1949, p. 229 et seq.) and increasing ossification with age, the feature is useful in separating skulls of adult pinnipeds when considering species on a suprageneric level. The magnitude of the differences override variation with age. The external limb of canalus semicircularis ossei anterior contacts and is closely appressed to the tentorium dorsoposteriorly, unlike Otariini and Arctocephalini in which the entire hummock containing the semicircular canals is free from the tentorium, and the cerebellar cavity is projected far posteroventroexternally. The aqueductus cochleae is bordered by a trough of bone posterodorsally as it opens into the cranial cavity; such a distinct trough is not developed in Otariini.

COMPARISONS WITH OTHER LIVING OTARIIDS

As I have found the middle ear region, particularly structures of the pars petrosa and pars tympanica, so useful in otariid systematics, the following comparisons consider mainly those regions.

Comparison of ear regions of I. downsi and Arctocephalini. — These comparisons are based on examination of the following specimens: *C. ursinus*, LACM M1699; *A. philippii townsendi*, LACM M1735, M2033, M1115a,b, and *A. australis galapagoensis*, LACM M1656. Most of the comments above noting differences between *I. downsi* and Otariini hold also for Arctocephalini, which are quite similar to Otariini. In *Arctocephalus* the vagina processus styloidei is variably open into the auditory cavity. The bulla is produced forward toward the glenoid fossa in some northern *Callorhinus*, as in some northern *Eumetopias*; backward and downward in more southerly *Arctocephalus* as in some southern Otariini. In *Callorhinus* the anterior horizontal septum roofs the canalis musculotubarius as in *I. downsi*, but floors the canal in *Arctocephalus* as in most Otariini. The globous space behind the small- to moderate-sized fenestra cochleae in *Arctocephalus*

is constructed like that in *Z. californianus* and *E. jubata* but evidently, unlike *I. downsi* particularly in being more inflated and spacious posteriorly, invading the processes projecting back from the auditory bulla. Most critical differences in the basicranial region are summarized in the diagnosis of Otariinae below.

Comparison of ear regions of I. downsi and O. rosmarus. — This comparison holds much interest, for it is assumed by many that the basicranial region is conservative and yields features of great use in phylogenetic studies. I have emphasized that odobenids, particularly *O. rosmarus*, might yield information on early otariids (Mitchell, 1966a) since they may represent a generalized otariid except for the specialized feeding mechanism (Mitchell, MS, 1967). Thus it may be that the features below found in both *O. rosmarus* and *I. downsi* were common to a number of early otariids and might be found in earlier, that is, more primitive, otariids. I have available only one dissected, dry skull, a young walrus LACM M702, and some intact adult skulls collected by Arthur Mansfield.

The basicranial region in *O. rosmarus* is similar in some details to that in *I. downsi*. There is no distinct posterior bullar projection in *O. rosmarus*, but the shape and position of foramen stylomastoideum, and the morphology of the groove (van der Klaauw, 1931, p. 176) running posterointernal behind the foramen to the vagina processus styloidei is markedly similar. However, the vagina in *O. rosmarus* is posteroexternal, not directly posterior, to the bulla. There are a number of differences in the region of the hiatus petrotympanicus, but foramen caroticus posterius opens in both species separately from foramen lacerum posterius, and less separately in Otariini (van der Klaauw, 1931, p. 189–190). The morphology of the entotympanic ventrointernal to canalis caroticus is almost identical. Anteriorly the bulla in *I. downsi* is flattened, but variably inflated in *O. rosmarus*. The postglenoid foramen in both species is large. In the region of the apical bullar spur and fossa in *I. downsi* there are remnants of possibly comparable, but smaller and less distinct, structures. Also the most posterior inframeatal spine in *I. downsi* is represented in *O. rosmarus* far dorsally on the posterior wall of the meatus acousticus externus, farther dorsoposteriorly than in most other otariids. It is not as distinct a spine as in *I. downsi*, however.

The bulla in both species is in general low, the mastoid is similar in shape, the paroccipital process is thin in both, the horizontal slope of squamosal above the meatus is similar, and in many other features similarities can be found. The paroccipital process is a thin plate of bone covering the back edge of the mastoid as in *I. downsi*, thus contributing to the mastoid flange as surmised by van der Klaauw (1931, p. 37, 101). The apparent distinction, that the periotic is visible behind the bulla in odobenines (evidently through foramen lacerum posterius) and not visible in Otariini (van der Klaauw, 1931, p. 123), does not hold as the periotic is visible in *O. byronia*.

van der Klaauw (1931, p. 71) stated that in *Odobenus* the largest axis of the tympanic membrane is almost exactly sagittal, but I find that in one juvenile skull (LACM M702) it is oriented anterointernoventrally about 35° from the sagittal plane, not significantly different from the condition in many other otariids.

Within the auditory cavity, the two species are similar in a number of significant structures: the septum canalis musculotubarius is moderately to well developed, the ventral lip of crista tympani is round and bulbous, the anterior horizontal septum of the entotympanic tends to roof the canalis musculotubarius, the entire auditory cavity is narrow and deep, there is a distinct eminentia vagina processus styloidei, and the tympanohyal contributes to the wall of the auditory cavity and even enters it directed toward the epitympanic recess. *Imagotaria downsi* and *O. rosmarus* are also similar in having a nearly circular membrana tympanica as attested by the shape of crista tympani.

Differences can be found in the shape of the facial canal distal to the genu, in the shape of elements in the bony roof of the auditory cavity, the rounding off dorsoanteriorly of the promontorium in *O. rosmarus* versus a horizontal flattening in *I. downsi* so that more of pars petrosa roofs the cavity in the latter, the horizontally wide fenestra cochleae in *O. rosmarus* that is low in height, and slight differences in the shape of recessus epitympanicus.

In *O. rosmarus* the entry of the tympanohyal into the auditory region is so complete that it contacts, and even becomes fused with pars petrosa at a point on the external wall of the facial

canal. Thus the tympanohyal actually contributes to the wall of the facial canal as well, lying ventroanterior to the facial nerve near where it turns ventroexternally to run between the tympanic and mastoid to emerge from the foramen stylomastoideum. van der Klaauw (1931, p. 176) has incorrectly stated that in adult walruses the tympanohyal is not distinct from the bulla, but has made an oblique reference to the true situation in stating that "the third part of the canalis Fallopii is formed by the mastoid, tympanic and probably also by the tympanohyal," a situation that might seem unique until it is remembered that the tympanohyal is one of the cranial-most ossifications in the second hyoid or branchial arch of mammals. The stapes also is derived from the cranial end of the second arch, hence the proximity of the two in the middle ear region (e.g. fig. 490, Goodrich, 1958). That is not to say that the persistence of the tympanohyal as a distinct, rod-like structure pointed toward the epitympanic recess is explained. Any laryngeal generation of noise is essentially at the end of the tympanohyal–stylohyal–epihyal–ceratohyal chain. An interesting speculation, in view of the extreme development of the vagina processus styloidei and associated structures in *I. downsi* and *O. rosmarus*, is that this hyoidean chain might serve as one possible route for sound transmission between the surrounding media and the middle ear. Whether the most distal, craniad tip of the tympanohyal is fused to pars petrosa, is partially or completely fused and buried more proximally within the wall of vagina processus styloidei, or is entirely free within the vagina is relatively unimportant to this speculation. It might still transmit sound if the interface between the tympanohyal and surrounding bones were distinct, and if the tympanohyal were of different density and internal structure. I suggest that a close look at the microstructure of the tympanohyal in comparison with surrounding bones would be useful, and that hypotheses concerning the hyoidean chain of bones as an alternative pathway for transmission of sounds become more attractive with the knowledge that at least one extinct sea lion, *I. downsi*, shows specializations suggestive of such function. I advance this hypothesis strictly as a speculation.

The tympanohyal lies in *O. rosmarus* as in *I. downsi* far dorsally at the level of membrana tympanica, its stylohyoid end thus being far within a cylindrical vagina processus styloidei. The vagina is consistently found in *O. rosmarus* as more of a distinct structure and less variable than in Arctocephalini and Otariini, approaching the specialized condition in *I. downsi* in some respects. The vagina opens into the auditory cavity in *O. rosmarus* through space around the tympanohyal, which is often fused to mastoid bone on its posteroexternal side.

In one young walrus (M702) it can be clearly seen that a part of the posterior wall of the auditory cavity is composed of pars mastoidea, as mentioned by van der Klaauw (1931, p. 286). Specifically, the mastoid crops out in the cavity internal to eminentia vagina processus styloidei. Since the vagina is removed in *I. downsi* far internally, directly posterior to the bulla and away from pars mastoidea, this relationship is precluded and the mastoid does not enter into the posterior bullar wall. I have not the materials to verify this in Otariini, but evidently in most species the mastoid probably does not enter the auditory cavity at this position.

Without the auditory cavity, on the cranial surface of pars petrosa, major resemblances are found in *I. downsi* and *O. rosmarus*. In both: the eminence containing the semicircular canals touches the crista petrosa and tentorium; the cerebellar fossa is deeper than wide; the bipartite nature of the petrosal is formed by a flattened, slightly striated surface dorsal, external and anterior to meatus acousticus internus and a thicker region ventrally continuous with the promontorium and divided by a sulcus and/or sharp, horizontal flange from the overlying part; the cranial orifice of aqueductus cochleae opens more dorsally and not so directed towards foramen lacerum posterius as in Otariini and Arctocephalini; the ball and socket junction of exoccipital and petrosal–mastoid is near the orifice for aqueductus vestibuli and the cerebellar cavity is not projected far posteroexternally; and other qualitative and quantitative similarities. Differences include: the pars petrosa is scooped out where it forms part of the external wallof the petrobasilar canal carrying the ventral petrosal sinus in *O. rosmarus* (and similarly in *E. jubata*, slightly in *O. byronia*, and not in other Otariini), but in *I. downsi* it is bulbous and inflated internally; and slight differences in proportions.

COMPARISON WITH EXTINCT OTARIINI AND REPUTED OTARIINI

The species *I. downsi* represents a very different kind of sea lion not heretofore known. In order to emphasize its distinctness, and demonstrate that it is not *P. magnus* (described on the basis of a braincase not strictly comparable with the Santa Barbara Museum specimen), the following survey of North Pacific fossil Otariini is offered.

Pontolis magnus True, 1905

The posterior part of a brain case with the pterygoids and part of the palatines (USNM 3792) comprise the holotype of "*Pontoleon*" *magnus* True, 1905a, but True (1905b) proposed the new generic name *Pontolis* to replace the preoccupied *Pontoleon*. The specimen had been collected in or previous to 1898 by B. H. Camman "in the sandstone bluff on the east side of the lower part of Coos Bay, between Empire City and the 'south slough' " (True, 1905a). True reported that this brain case came from the "Empire beds" which evidently referred to the Empire Formation, in this region considered by Weaver et al. (1944, chart 11) as early to middle Pliocene in age.

True (1909) compared *P. magnus* with *E. jubata* and suggested that the fossil species was ancestral to the living species. Kellogg (1925b) referred a foot from rocks in Soledad Canyon, Los Angeles County (rather than San Diego County, as stated by Kellogg in the title and throughout his paper) and an additional metatarsal from the same region to *P. magnus* because the "specimen is no doubt very closely related to the genus *Pontolis*, possibly the same form as True described, since the skeleton is unknown" (Kellogg, 1922, p. 60). I here regard the number of "structural modifications peculiar to the Odobenidae" found by Kellogg (1925b) more important and indicative of generalization, hence term the foot (UCMP 24070-24082) "Otariidae undet." and refer the associated metatarsal (UCMP 24083) to the same species. Lyon (1941) referred to the species *P. magnus* a partial, distorted skeleton of a large pinniped from Lomita, California, which has been discussed in a separate section below.

Comparison of the skull of I. downsi with the holotype of P. magnus. — According to True (1909) the basicranial region of the holotype of *P. magnus* (USNM 3792) was poorly preserved. I find upon examination of the holotype that there has been no major distortion not readily apparent in the form of large cracks, and that the bullae in the holotype are not crushed but normally smooth and flat as in females of *P. hookeri*. Dr R. Kellogg wishes to keep the specimen in the condition in which True described it. Differences of some aspects of the size and shape of the paroccipital–mastoid flange will not be emphasized as they may be related to a wide range of age, sex, or individual variations. In the holotype of *P. magnus* the glenoid fossae do not tilt dorsointernally to any significant degree as they do in *I. downsi*; the auditory bullae are even flatter and show no indication of an apical bullar spur and fossa on the surface ventral to the external auditory meatus; the paroccipital–mastoid wing projects laterally whereas in *I. downsi* it projects more ventrally; the paroccipital end of the wing may extend back farther; there is no indication of a posterior bullar projection on the bulla although its absence might be an artifact of preservation; and the transverse ridges between the postglenoid foramen and the bulla are not accentuated. The holotype of *I. downsi* and that of *P. magnus* can be compared in the width across the palatine bones at the end of the hard palate, expressed as a percentage of the least distance from the posterodorsal corner of the paroccipital to the posterior surface of the glenoid fossa. The ratios (see Table II) are about .75 for *I. downsi* and .60 for *P. magnus*. The same ratio for the referred specimen of *I. downsi* is estimated to be at least .66 and possibly up to .69. Other proportional differences, derived from the referred specimen (USNM 13487), include: the ratio width across braincase at level of glenoid fossae/paroccipital width is .83 vs. .53 in *P. magnus*; and the ratio auditory width/paroccipital width is 1.00 vs. .95 in *P. magnus*. I conclude that *P. magnus* is distinct from *I. downsi*.

Comparison with Oregon specimens of unknown identity. — It will be seen that *P. magnus* is still known only from the holotype, the back end of a large skull. The following argument may be pertinent: *P. magnus* was determined by True to be similar in many respects to *E. jubata*. A fossil mandible (UOMNH 1938) was described by Shotwell (1951) who recognized that it

might be referable to *P. magnus*. As this jaw came from a conglomeratic lense (UOMNH locality 42) in the Empire Formation in Coos Bay, the same area and the same unit as the holotype of *P. magnus* (Shotwell, 1951), it is possible that it represents the same species (Shotwell, 1951). Two large species of otariids are sometimes found in the same region, but the usual case is an association of large Otariini and smaller Arctocephalini (cf. maps in Scheffer, 1958). It is possible that the Oregon fossil jaw represents a second large species of otariid that lived contemporaneously in the vicinity occupied by *P. magnus*. The short jaw is notable in having five functional, shallowly rooted postcanine teeth with round roots, and in having only one small incisor which is appressed to the anteromedial side of the lower canine. These characters alone clearly separate it from *I. downsi*. Increasing the probability that this jaw represents *P. magnus* is the discovery of another rostral fragment (UW 22359) from the same or a neighboring locality (UW 2730) in the conglomeratic lense in the same unit. This snout fragment shows single, round-rooted premolars and only one pair of round-rooted incisors between the enlarged I3/. This snout, and the jaw mentioned above, must be from the same species on the basis of reduction of number of incisors and shape of postcanines alone. The dentition serves to sharply separate it from *I. downsi*, but it is a moot point at present whether the species represented is *P. magnus*. These fossils will be described and illustrated in detail in a subsequent paper.

Comparison of the holotype of I. downsi with Doheny Beach squamosal. — A squamosal bone collected by Carl Weidert in 1963 from the cliffs north of Doheny State Park, south of Dana Point, Orange County, California, might represent *P. magnus* or some other large otariid pinniped. The squamosal (LACM 8915, locality 1950) is much larger absolutely than the Lompoc squamosal. The *I. downsi* holotype has a relatively smaller mastoid area; a large spur of bone is present on the ventrolateral lip of the external auditory meatus (although a smaller, comparable spur is to be found on the Doheny Beach bone); and the auditory bulla is slightly more inflated. But more telling differences can be found that are not associated with age, sex, or possibly individual variations. The eminentia vagina processus styloidei is a prominent feature in the posterior end of the tympanic cavity in the Lompoc squamosal. It is bulbous and thin walled, projecting forward into the hypotympanicum as a vertical swelling, extending dorsally toward the epitympanic recess. In the Doheny Beach bone, vagina processus styloidei extends from near the posterior end of the auditory bulla through the wall and opens toward the epitympanic recess but is not produced into a ridge or eminence of any kind internally. The eminentia vagina processus styloidei is without marked relief on the posterodorsal wall of the hypotympanicum. The crista tympani in the Doheny Beach specimen has a ventral margin that overhangs the hypotympanicum markedly, and two major struts run anteroventrally and posteroventrally, respectively, from this crista. In the Lompoc bone, the crista does not overhang the hypotympanicum with a downhanging crest, and there is a single, major vertical strut extending beneath it on the wall of the hypotympanic sinus. In the Lompoc squamosal the ridge of bone behind the postglenoid foramen is thicker; the dorsal lip of the eminentia vagina processus styloidei is projected as more of an arcuate crest; and the stylomastoid foramen is more ovate than round as in the Doheny Beach fossil. A posterior bullar projection may, or may not, have been present as the critical region is broken in the Doheny Beach squamosal. The edge of the bulla nearest the mastoid ridge is produced into a downhanging, rugose crest, whereas in the Lompoc specimen a smooth, laterally directed ridge is found here. The ventral surface of the auditory bulla is relatively flat in the Doheny Beach squamosal, particularly out toward the external auditory meatus. Decidedly different, the Lompoc specimen has a major spur of bone on the ventral surface of the bulla, between the mastoid crest and the postglenoid process, directed externally, and ventral to the lip of the external auditory meatus. This apical bullar spur underlies an apical bullar fossa of considerable depth. These structures are completely unlike the flattened bulla of the Doheny Beach fossil. The ventral surface of the bulla in the Doheny Beach squamosal shows a pronounced ridge running anteromedially, where it conforms to the course of the auditory tube. There is no comparable ridge on the Lompoc bulla. Other direct comparisons of these two specimens are difficult owing to differences in preservation. The length from the most posterodorsomedial point of the hypotympanicum to the posteroventral lip of the foramen caroticus externus (measurement *a*) is about 43.0 mm in Doheny Beach (foramen caroticus externus position uncertain),

and about 30.0 mm in Lompoc. A few other measurements can be made: *b*, ventral edge of crista tympani to most medial curve of dorsal lip of external auditory meatus, 64.5 mm in Doheny Beach, 40.0 mm in Lompoc; *c*, height from apex of epitympanic recess to floor of hypotympanicum, 32.0 mm in Doheny Beach, approximately 26.5 mm in Lompoc; *d*, anterodorsal edge of meatal tube at sulcus tympanicus to posterodorsal lip of posteriorly opening vagina processus styloidei, 36.5 mm in Doheny Beach, 22.0 mm in Lompoc. The ratio *c*/*a*, reflecting relative height of tympanic cavity, is about .74 in Doheny Beach vs. .88 in Lompoc, showing that the tympanic cavity in the Lompoc squamosal is relatively much deeper. Other ratios like *a*/*b* show that in Doheny Beach (.67) the crista tympani is at the end of a relatively longer meatal tube than in Lompoc (.75); and the ratio *d*/*a* of .85 in Doheny Beach vs. .73 in Lompoc indicates that the external mouth of the vagina processus styloidei is farther posteriorly from the crista tympani than in Doheny Beach.

Comparison of the holotype of I. downsi with dentition of "cf. Pontolis magnus" from Lomita. — Lyon (1941) attempted to describe a partial, distorted sea lion skeleton from diatomites on the inland side of the Palos Verdes Hills near Lomita, California. Additional locality data is not to be found in her paper, but Downs (1956) stated that it is in the Valmonte Diatomite Member of the Montery Shale, of late Miocene age. The Valmonte Diatomite overlies and is interbedded with the Altamira Shale, and both units are considered members of the same formation. Another sea lion has been described by Downs (1956), from the Altamira Shale, and its occurrence raises the possibility that the two specimens might represent the same species. Downs' skeleton represents a species, *Allodesmus* (*Atopotarus*) *courseni*, related more to desmatophocine pinnipeds than to otariines. The cheekteeth, insofar as can be determined, bear no major lingual cusp as in the Lyon specimen and there are other significant differences. The two seem to represent different kinds of animals. Lyon's description is an uncritical account of the state of preservation of the skeleton; from three pages of this account I have gleaned the following: sagittal crest present, paroccipital–mastoid process heavy and broad, zygomatic arch massively constructed, mandibular fossa long anteroposteriorly with pronounced posterior flange, supraorbital processes absent, auditory bulla triangular, palate long with transverse margin posteriorly, mandibular symphysis unfused, canines wear with age, three upper and two lower incisors, "first premolar" single rooted, "second premolar" incipiently double rooted, "third premolar" possibly double rooted, more posterior teeth certainly double rooted, some postcanines with anterior and posterior and possibly internal accessory cusps, cingulum present on some postcanines, last molar may be three rooted, and radius shorter than humerus. Even these conclusions are suspect as the specimen has not been completely prepared. However, I borrowed the skull, the left jaw fragment, and the teeth from the Los Angeles County Museum (where the specimen is now catalogued as LACM 4324) and after first taking a plaster cast of the right basicranial area, cut into the auditory bulla but found the middle ear region so broken and distorted that any conclusions that might result from its study would be suspect. The following comments and comparisons are based upon only a study of these elements, mainly the teeth. I have previously prepared and commented upon the humerus of this skeleton (Mitchell, 1961, p. 13). The bones of the tarsus should be prepared and compared with the supposed foot of "*Pontolis magnus*" described by Kellogg (1925b). The entire skeleton should be prepared with a small sandblaster and completely described and compared.

I have assigned letters to the parts of the skeleton in order to discuss the individual teeth. These teeth and bones, as I have identified them, include (with Lyon's plate and figure numbers in parentheses after those illustrated): LACM 4324*a*, a possible upper left PC6/ if *j* is PC5/ (Lyon, 1941, fig. *a* and *b*, pl. 2, fig. 1 and 3, far right); *b*, a lower or upper medial incisor where *c* is the opposite tooth, not a "rudimentary molar or premolar" (fig. 2*c* and *d*, pl. 2, fig. 1 and 3, second from right); *c*, a lower or upper medial incisor where *b* is the opposite tooth (pl. 2, fig. 1 and 3, first on left); *d*, a questionable left PC/1 (pl. 2, fig. 1 and 3, second from left); *e*, a right PC2/ where *i* is the opposite tooth (pl. 2, fig. 1 and 3, third from left); *f*, a right PC1/ (pl. 2, fig. 1 and 3, third from right); *g*, a lower or upper medial incisor that would be external to *b* or *c* if all were uppers (pl. 2, fig. 2 and 4, first on left); *h*, a right PC/3 (pl. 2, fig. 2 and 4, second from left); *i*, a left PC2/ where *e* is the opposite tooth (pl. 2, fig. 2 and 4, third from left); *j*, a left PC5/ if *a* is PC6/ (pl. 2, fig. 2 and 4, fourth from left); *k*, a questionable left PC4/ (pl. 2, fig. 2 and

4, fifth from left); *l*, a left PC3/ (pl. 2, fig. 2 and 4, first on right, top); *m*, tip of root of PC not necessarily of *l* (pl. 2, fig. 2 and 4, first on right, bottom); *n*, anterior fragment of left lower jaw with PC/2–PC/3 in place (pl. 3, fig. 5 and 6); *o*, anterior fragment of right lower jaw (pl. 3, fig. 7); *p*, fragment of skull containing right I2/–I3/ in place (pl. 3, fig. 8); *q*, fragment of skull containing fragment of left I2/ and I3/ in place (pl. 3, fig. 9); *r*, distorted skull (fig. 1); *s*, probable left lower canine; *t*, crushed right humerus (pl. 4, fig. 10; and Mitchell, 1961, fig. 10); *u*, fragment of ulna (pl. 4, fig. 10); *v*, radius (pl. 5, fig. 12); *w*, proximal end of tibia (pl. 4, fig. 11); *x*, block of diatomite containing partial lower leg and pes (pl. 6, fig. 14); *y*, fragment of innominate; *z*, scapula; *aa*, atlas, cervical vertebrae, and sacrum; *ab*, patella (pl. 5, fig. 13).

It will be seen that some duplication occurs, and that therefore *s*, probably a left lower canine, is from another, smaller individual of the same species. The questionable left PC/1 (*d*) may be from another individual or may be incorrectly allocated to its position in the jaw. The left PC3/ may be from a smaller individual as it is nearly the same size as that in the Santa Barbara Museum palate, which is less than two thirds the length of that in the Lomita skull. The above placement of the teeth in the jaws is based mainly upon comparison with the jaws and teeth of the Lompoc specimen (SBMNH 342) and with the relatively unworn teeth in a skull of *P. hookeri* (BM (NH) 1851.7.18.48) and a skull of *N. cinerea* (1925.10.8.32). The following description of the teeth associated the Lomita specimen also compares the teeth with those of the Santa Barbara specimen, *I. downsi*. The supposed incisors (LACM 4324*b*, *c*, *g*) have relatively short roots that are ovate in section as in the Santa Barbara animal, and not so flattened from side to side as in modern Otariini. The crowns are worn or broken away, but evidently were relatively low and bulbous. If they were upper teeth, it is not known whether they were grooved transversely or not. The roots of *b* and *c*, a matched pair of supposed incisors, have a small groove on each side. The upper third incisors have a sulcus on their external root surfaces, and a pronounced ridge on the posterior edge of the crown. The upper second incisors had a slight sulcus on the internal surface of the root. There were two lower incisors. The canines are large, have a distinct groove on each side (at least the lower left canine does) and the lower canines are greatly worn on the posterior surface where they contact the anterior surface of the upper canines. There is some vertical fluting on the internal surface of the crown of the left C/1. The upper right canine has a sulcus on the external root surface. The upper postcanines are completely represented in the sample as I have identified them above. The right upper postcanine (4324*f*) has a long root that slopes posterodorsally, is round in section with a slight sulcus on the external side of the root and has a crown shaped much as in living Otariini except that there is no well-defined external or internal cingulum and there is a single accessory cusp posteroexternal to the main cusp. A marked bulge lies on the internal, dorsal margin of the cusp in place of a defined cingulum, giving the appearance in anterior view that the main cusp is offset externally on the crown base. A ridge runs from the cusp tip to the accessory spur.

The teeth, with enlarged cingula, incipiently or fully bipartite roots, and accessory cusps are unlike those of Otariini but like those of *I. downsi*. On the basis of such similar dentition, *I. downsi* and the species represented by LACM 4324 are clearly related. The referral of LACM 4324 by Lyon to *P. magnus* is debatable, but if ultimately found to be correct then *P. magnus* and *I. downsi* are related in having common features in the dentition.

Pliopedia pacifica Kellogg, 1921

This species, known certainly from only one specimen, the holotype of which is unavailable, was referred to the Odobenidae by Mitchell (1966a) in contrast to its original description as an otariid by Kellogg (1921). Known from supposed Late Pliocene rocks in central California, the holotype of the species *Pliopedia pacifica* and the holotype of *I. downsi* contain only one bone in common, the humerus. Comparison of the figures of the distal end of the *P. pacifica* humerus and that of *I. downsi* show similarities such as the relatively great anteroposterior diameter of the internal edge of the trochlea for the ulna and the reduced olecranon and coronoid fossae. They differ significantly in the shape of the deltoid crest which is thinner and drops off more abruptly distally in *P. pacifica*; in the robustness of the shaft distally, more robust in *I. downsi*;

in the size of the ectepicondyle which is diminished in *I. downsi*; and in the shape of the external edge of the capitulum for the radius. The capitulum runs up almost as far proximally onto the shaft in *P. pacifica* as the trochlea, much less so in *I. downsi*. The two species are clearly distinct on the basis of these differences.

Allodesmus kernensis, nec *Eumetopias sinanoensis* Nagao, 1941

Nagao stated that the snout of "*Eumetopias sinanoensis*" differed from that of *Allodesmus* (as known to Nagao only through Kellogg, 1922, not Kellogg, 1931) "in having apparently a slightly deeper horizontal ramus, almost unworn teeth, a rather smaller canine, and a larger lower outer incisor, than in *Allodesmus*. All the premolars are also relatively larger in the Japanese form than in *Allodesmus*, with the roots more regularly circular in cross-section." But these are minor differences for the most part, and comparison of Nagao's photographs of the distorted snout with isolated teeth (LACM 10295–10298 for example) and a skull (LACM 4320) of *Allodesmus* shows no major apparent differences, and the Japanese specimen should be provisionally referred to that genus instead of *Eumetopias*. Since the lower inner incisors are only "situated a little posterior" to the outer incisors, and because the "inner incisors seem to be almost parallel with the outer ones" (Nagao, 1941, p. 78), this specimen is best referred to *Allodesmus kernensis* (sensu Mitchell, 1966a) and *E. sinanoensis* Nagao, 1941, is accorded synonymy with *A. kernensis*. Hopefully this referral will stimulate further preparation and restudy of the specimen.

Eumetopias watasei Matsumoto, 1925

Described in Japanese on the basis of a snout fragment in 1925 (Matsumoto, 1925) and later redescribed and refigured in English (Matsumoto, 1926), the species *Eumetopias watasei* was separated from *E. jubata* because the first and second incisors were relatively much larger and because at least the first two premolars were round rather than oval. Certainly, as judged from the figures (Matsumoto, 1926, pl. 6) the snout anterior to the canine is relatively longer than in the specimen of *E. jubata* used for comparison, and the alveolus for I1/ lies entirely forward of the alveolus for I3/.

Comparison of the figures of the holotype of *E. watasei* with skulls of otariids kindly loaned through the courtesy of Miss J. E. King of the British Museum (Natural History) emphasizes the above differences. The skulls (*Otaria byronia*, 1959.12.4.6; *Neophoca cinerea*, 1925.10.8.32; *Phocarctos hookeri*, 1851.7.18.48; *Zalophus californianus*, 1903.10.11.1; and *Arctocephalus australis*, 1950.11.14.4) all differ from the holotype of *E. watasei*, in which the palate is flatter, the incisive foramen is relatively larger, the roots of the cheekteeth are rounder (except that *O. byronia* has relatively round cheek tooth roots also), and the lateral profile slopes more gently out to a more elongated snout. The diastema between the lower canine and the third incisor is small in *O. byronia* (LACM M1715, M1610), relatively longer in *E. jubata* (LACM M756, M551) and much longer in the holotype of *E. watasei*. Among some Arctocephalini the medial incisor is relatively far forward, but never more than beyond the level of the anterior one-third of the I3/ alveolus, as in *E. watasei*. The elongated snout of *E. watasei* is like that found in *Z. californianus* and some Arctocephalini but the tooth characters are more like those in *E. jubata*. Because of the distinctness of *E. watasei* and the fact that it is less similar to *E. jubata*, *O. byronia*, and *Z. californianus* than these species are to each other, I propose a new genus for receipt of Matsumoto's *Eumetopias watasei*:

Oriensarctos new genus

The type species of *Oriensarctos* new genus is *Eumetopias watasei* Matsumoto, 1925. The holotype of the species is a fragment of the right side of the snout (Matsumoto, 1925, pl. 3; 1926, pl. 6) of an otariid skull collected from "a bed of coarse-grained sandstone, probably of the Sanuki Formation of the Narita Series" in "Megakura, Umegase Valley, Province of Kazusa,"

Japan. The generic name is in reference to the eastern occurrence of the species. *Diagnosis* of the species *Oriensarctos watasei* is: an otariid pinniped that has single and round rooted PC1/–PC2/, snout long, alveolar diameter of I3/ almost as large as canine, root of I3/ round, roots of I1/ and I2/ relatively round, alveolus of I1/ entirely anterior to alveolus of I3/ and the palate relatively flat.

Comparison of *Oriensarctos watasei* with *I. downsi* (SBMNH 342) reveals that the Santa Barbara species differs in most of the same ways from *O. watasei* as does *E. jubata* and *O. byronia*. In the holotype of the Santa Barbara species the palate is more arched, the snout is shorter, the I1/ and I2/ are aligned from side to side and not staggered, the PC2/ and PC3/ are incipiently or completely double rooted and not single rooted, the incisive foramina send forward a sulcus unlike the Japanese fossil, I3/ is oval in section and not round, and so on. The two are plainly distinct.

Eumetopias sp. ?, *nec* "*Allodesmus* sp.," *nec Eumetopias jubata*

I concurred with Shikama's (1953) reidentification as *E. jubata* of the Pliocene sea lion jaw originally described by Kaseno (1951) from Kanazawa as "*Allodesmus* sp." (Mitchell, 1966a, p. 19). However, comparison of a cast of the mandible (now in the LACM) kindly supplied by Dr Kaseno discloses that it differs from a jaw of *E. jubata* (LACM M756) in having a more massive anterior end. It is particularly swollen on the medial surface behind the symphysis, approaching but not identical with the condition in a jaw of *O. byronia* (BM(NH) 1959.12.4.6). I now suggest that this Pliocene jaw be studied further before being unequivocally identified as conspecific with *E. jubata*. The cast shows that the medial incisor sat in an alveolus posteromedial to the I/2, which was seated in an alveolus closely adjoining the canine. The first three premolars were single rooted and the roots were nearly round in cross section, but the PC/4 and PC/5 were incipiently or completely double rooted, unlike *E. jubata* (LACM M756). The second molar is completely missing and has evidently been lost in this species, but the cast does show a slight scar in the area where an alveolus for PC/6 might have been.

This jaw differs considerably from the jaw of *I. downsi* in having no genial tuberosity, no PC/6, an ovate rather than a rhomboidal symphysial surface, and in being deeper dorsoventrally at the level of PC/2 rather than at the level of PC/6.

Zalophus californianus, *nec Eumetopias* (?) *kishidai* Shikama, 1953

Based upon a fragment from the tip of the snout, this supposedly extinct species is of unknown age and from a locality "unknown precisely." Shikama (1953) reported that it came from "diluvial drifts in Tokyo" but he proposed instead that it might have come from Pliocene deposits in the Umegase district of Japan. Shikama concluded that the species was distinct on the basis of the protrusion of the tip of the snout far beyond the incisor tooth row. From an examination of the figures (1953, pl. 2) I submit that the combination of the strongly protruded snout tip and the anteroventrally (rather than ventrally) directed canine identifies this fossil as a species of *Zalophus* (e.g. compare Sivertsen, 1954, pl. 1–7). Shikama's idea that the fossil represents a small-sized sea lion would corroborate this conclusion. The shape of the incisive or anterior palatine foramina differs from that figured by Sivertsen (1954, pl. 3) but this is highly variable in *Z. californianus* (sensu Scheffer, 1958), for incisive foramina like that in the fossil are found in LACM M489, the skull of an adult male, and compare Mori, 1958, pl. 1 for a possible Japanese example that is similar.

Until such time as more information regarding the provenance of this fossil is available and it is more critically compared with skulls of *Zalophus*, to demonstrate differences, I propose that *Eumetopias* (?) *kishidai* be relegated to synonymy with *Z. californianus*. These features in which it resembles *Z. californianus* and differs from *E. jubata* serve also to distinguish it from the new species described herein. Whether the Japanese fossil had a small protrusion on the anterior wall of the external nares (halfway up the side) is not clear: if this spur was naturally

absent and not abraded away, perhaps it would serve to distinguish the fossil from *Z. californianus* and would suggest similarities to species of *Arctocephalus*.

Zalophus kimitsensis Matsumoto, 1939

Based upon a fragment of a mandible from the "*Parelephas protomammonteus typicus* Zone; Basal Calabrian," Matsumoto (1939) named this new species of *Zalophus* because it had a small canine relative to length of postcanine tooth row. As the canine size in *Zalophus* is variable and related to sex and age, I regard the validity of this species with scepticism but have no translation of the original paper or a clear enough copy of the illustration to offer critical comments. The specimen should be restudied and compared with a series of jaws of *Z. californianus*.

COMPARISON WITH SELECTED OTHER EXTINCT OTARIIDAE

Information presented in comparisons is supplemented in the diagnoses of the various subfamilies below. These comparisons show that *Imagotaria downsi* is as different from Otariini and Arctocephalini as from *Desmatophoca oregonensis*, *Allodesmus kelloggi*, and *Dusignathus santacruzensis*.

Comparison of the ear regions of I. downsi and holotype of Desmatophoca oregonensis. — Dr J. A. Shotwell has kindly allowed me to borrow and prepare the holotype (UOMNH F-735) of *Desmatophoca oregonensis* Condon, 1906, from the middle Miocene Astoria Formation along coastal Oregon. It will be described in detail in a forthcoming report. *Desmatophoca oregonensis* differs from *I. downsi* in many important ways: the paroccipital forms a separate process not fused with the mastoid; the meatus acousticus externus is not floored so far externally by the ectotympanic, not beyond the level of foramen stylomastoideum; the mastoid process is relatively small, rugose tip does not extend posterior to foramen stylomastoideum; the meatus acousticus externus is directed anteroexternally about 33° from a transverse axis; the axis of the auditory bulla is directed anterointernal 40° from a longitudinal axis; there is no enlarged foramen postglenoideum; the internal, ventral edge of the bulla hangs far below the internal basicranial surface; the internal lip of foramen caroticum posterius is composed of entotympanic and not basioccipital; the posteroexternal edge of the bulla borders the paroccipital, not the mastoid, process, and its surface is continuous with it, not separated by a sharp-edged bulla; there is no groove between foramen stylomastoideum and vagina processus styloidei; there is no posterior bullar projection; there is neither an apical bullar spur nor an apical bullar fossa; there are no inframeatal crests, ridges, or spine; the auditory bulla is smooth and flask shaped with its longest apex anterointernally, no apex externally under meatal tube; and the entotympanic is not perforated by numerous foramina for circulatory system but smooth. Within the auditory cavity differences can be seen in the shape of the promontorium which projects far ventrally, is irregularly globous but small, and does not extend far anteriorly; in the slight degree to which the canalis caroticus bulges into the auditory cavity; and in the flattened crista tympani which is oriented almost vertically and does not project into the auditory cavity.

The two species are similar in having an auditory bulla inflated only far behind the glenoid fossa, with a shallow excavation behind the internal end of the postglenoid process; the vagina processus styloidei present; a similarly shaped dorsointernal edge of fenestra cochleae; and a deep auditory cavity with hypotympanicum enlarged. The two species differ greatly, but given some of the trends known within Otariidae, many conditions in *I. downsi* could have been derived from those in an ancestor like *D. oregonensis*.

Comparison of the ear regions of I. downsi and holotype of Dusignathus santacruzensis. — There is little to compare between *I. downsi* and *Dusignathus santacruzensis* Kellogg, 1927, as the temporal bone of the latter is broken and only a fragment of pars petrosa remains (UCMP 27121). *Dusignathus santacruzensis*, first called a sea lion (Kellogg, 1927), was found in the Pliocene Purisima Formation (Mitchell, 1962) in coastal central California, and has been considered a good structural step between *Allodesmus* and *Prorosmarus*, notwithstanding its true phyletic relationship, probably paralleling living walruses (Mitchell, 1966a). It is similar to *I. downsi*

TABLE V. Tabular comparison of critical cranial features used in subdividing the Family Otariidae (new sense). Other characters are also of importance, but these quickly give a broad view of the differences between units such as subfamilies.

Feature	Desmatophocinae	Odobeninae	Dusignathinae	Allodesminae	Imagotariinae	Otariinae
Mandibular symphysis in adult	Unfused	Fused	Unfused	Unfused	Unfused	Unfused
Squamosal — jugal contact	Squamous ?	Squamous	Squamous	Mortised	Squamous ?	Squamous
Upper canine	Caniniform	Tusk	Caniniform	Caniniform	Caniniform	Caniniform
Lower canine	Caniniform	Premolariform	Caniniform	Caniniform	Caniniform	Caniniform
Postcanine roots at middle of tooth row	Double rooted	Single rooted	Single rooted	Single rooted	Incipiently double rooted	Incipiently double rooted
Postcanine cingular cusps	Small to absent	Absent ?	Absent ?	Small to absent	Enlarged	Small to medium
Projection of paroccipital process	Posteriorly	Ventrolaterally	Ventrolaterally	Posterolaterally	Ventrolaterally	Ventrolaterally
Relation of paroccipital process to mastoid process	Separate	Continuous	Continuous	Separate	Continuous	Continuous
Size of foramen lacerum posterius	Small to medium	Medium to large	–	Small	Small	Large
Auditory bulla	Inflated, smooth	Inflated, smooth to rugose	Flat, smooth	Flat, wrinkled	Flat, smooth	Inflated, smooth to rugose
Apical bullar spur and fossa	Absent	Small	–	Absent	Present	Small to absent
Inframeatal rim	Smooth	Spinose	Slightly spinose	Wrinkled	Spinose	Spinose
Vagina processus styloidei position relative to bulla	Posterolateral	Posterolateral	Posterolateral	Posterior	Posterior	Posterolateral
Vagina processus styloidei connected by groove with foramen stylomastoideum ?	No	Yes	No	No	Yes	Often
Labrum vagina processus styloidei present ?	No	Sometimes	No	No	Yes	Sometimes
Posterior bullar projection	Absent	Absent ?	Absent ?	Absent	Present	Present ?

Eminentia vagina processus styloidei	Small	Moderate	Small?	Small to absent	Enlarged	Small to moderate
Foramen caroticum posterius and foramen lacerum posterius	Separate	Separate	–	Separate	Confluent	Often confluent
Recessus meatus acousticus externus	Absent	Small	Small	Absent	Small	Small to medium
Crista tympani projects into auditory cavity, with free ventral edge?	No	Slight projection no overhang	Slight projection no overhang	No	Slight projection no overhang	Yes
Membrana tympanica	Round, small	Almost round, large	Subquadrate, large	Round, small	Almost round, large	Ovate, large
Pars petrosa, dorsal to meatus acousticus internus	–	Striated, flattened	–	Striated, flattened	Striated, flattened	Rounded, smooth
Fossa cerebellaris deeper than transverse width of entrance in adult?	–	Sometimes	–	Yes	Yes	No
Tentorium appressed to eminence for semicircular canals?	–	Yes	–	Yes	Yes	No

in having an inframeatal crest; a meatus acousticus externus floored by ectotympanic out to between the postglenoid process and the rugose tip of the mastoid process, well beyond the foramen stylomastoideum; a relatively flat auditory bulla with a smooth surface; a relatively large postglenoid foramen; and the bulla low and uninflated anteriorly behind the postglenoid process. The presence of an apical bullar fossa in *D. santacruzensis* is questionable: there is a large crack running transversely through the region, but the surface on the anterior edge of the crack seems to naturally slope dorsalwards in the area an apical bullar fossa might be expected. It appears to me as if a small fossa may have been present, but this must be confirmed with additional specimens. Within the auditory cavity similarities can be found like: the crista tympani projects into the auditory cavity; the epitympanic recess is moderate in size; the membrana tympanica was of large diameter; the hypotympanicum is moderate to deep and extended well behind the promontorium; the vagina processus styloidei is present, lays far posterointernal to foramen stylomastoideum, may open via a canal into the auditory cavity anterior to the facial canal and pointing dorsoexternoanteriorly toward the epitympanic recess; and the fossa incudis of the epitympanic recess is narrow and extends posteriorly beyond the level of the posteroexternal edge of the promontorium.

Dusignathus santacruzensis differs from *I. downsi* in having no groove between foramen stylomastoideum and vagina processus styloidei but a smooth surface continuous from bulla to mastoid flange; no major crests parallel to and behind the postglenoid process; a lightly built, not massive, postglenoid process that does not extend far ventrally; no struts or "rafters" radiating from crista tympani on external wall of auditory cavity; a membrana tympanica that was subquadrate in shape, with a distinct corner anteroventrally, rather than round; an eminentia vagina processus styloidei that is reduced or absent; possibly a canalis musculotubarius of larger diameter; and less of a bulge beneath crista tympani.

The two species are more similar than not in the conformation and relationships of important structures, differing mainly in those features that are specializations in *I. downsi*. They are plainly related to some degree, but insofar as can be determined *D. santacruzensis* retains a number of features found also in *Desmatophoca oregonensis*. *Imagotaria downsi* and *D. santacruzensis* are related through some earlier common ancestral stock, but the two species have diverged and become specialized.

Comparison of the ear regions of I. downsi and holotype of Allodesmus kelloggi. — The holotype of the middle Miocene otariid *Allodesmus kelloggi* is a complete skeleton (Mitchell, 1966a), the skull of which has been dissected to show details within the auditory cavity. There are some pronounced differences between *A. kelloggi* and *I. downsi*, as well as marked similarities. The two species are similar in having: a vascularized entotympanic bone; a flattened auditory bulla; a distinct vagina processus styloidei, posterior to the bulla; a slight groove from foramen stylomastoideum towards, but not reaching, the vagina; the foramen caroticus posterius opening separately from foramen lacerum posterius; the tentorium appressed to the eminence containing the semicircular canals; the cerebellar cavity not projected far posteroexternally; the cerebellar fossa is deeper than the width of its mouth; a slightly bipartite pars petrosa involving a dorsal, flattened part and a ventral, more bulbous portion; a large, wide fenestra cochleae; an enlarged globous space behind fenestra cochleae; a membrana tympanica that was round; the meatus acousticus externus underlain by ectotympanic out beyond the level of foramen stylomastoideum; and other major resemblances that confirm a degree of phyletic relation between *A. kelloggi* and *I. downsi*.

Allodesmus kelloggi differs in having: a thick paroccipital, contributing to a paroccipital process separate from the mastoid process; no inframeatal spines; no apical bullar spur or fossa; the periotic visible ventrally through the foramen lacerum posterius; foramina of differing size and different proportions in the pyramid posterior to meatus acousticus internus; a wide entotympanic, thickened around canalis caroticus; a shallow, but large bore, vagina processus styloidei; a less spaceous auditory cavity with its long axis almost at a right angle to the axis of canalis musculotubarius; the entotympanic, anterior horizontal septum contributing to the floor, not the roof, of canalis musculotubarius; a promontory inflated anteriorly and hanging more ventrally into the auditory cavity; an epitympanic recess that is not as distinctly demarcated,

and situated more anteriorly, with fossa incudis not extending back beyond the transverse level of the back edge of fenestra vestibuli; a major strut from the entotympanic, internal wall of the bulla projecting posteroexternally to underlie the ventral apex of the promontorium, unlike any comparable structure in *I. downsi*; no well-developed septum canalis musculotubarii; a narrowly constricted canalis musculotubarius; a vascularized internal wall of the auditory cavity which is extremely thick between the cavity and canalis caroticus; a crista tympani that does not project appreciably into the auditory cavity; a membrana tympanica of small diameter; a low, weak eminentia vagina processus styloidei; and the tympanohyal lying exposed on the posteroexternal wall of the auditory cavity. Some of these major differences demonstrate that *A. kelloggi* and *I. downsi* were on two separate phyletic lines. They must have been related, distantly, through a common ancestral stock, such as Desmatophocinae or a group akin to it.

OTARIID PHYLOGENY

It has long been assumed that some group of the Otariidae gave rise to the Odobeninae in the North Pacific. The North Pacific is as likely a region as any for this to have occurred and all of the Middle Miocene and later Tertiary fossil evidence for this argument has been found in this basin. But I find the assumption to be not yet proven. In a 1912 review of the accomplishments of the preceding decade, True stated that the hypothesis that walruses were derived from some primitive form of sea lion was at that time a point inferred but not demonstrated.

It appears to me that too much emphasis has been placed upon the obvious specializations of the living walrus — most of the specialized cranial features can be correlated with the dominance of canine tusks in the upper jaw. Thus it would seem that the reduction of the lower canines to crushing teeth similar to the premolars, symphysial fusion of the dentary bones, incorporation of an incisor into the upper crushing tooth row, massiveness of the cranium and many other specializations are all part of an interrelated set of features resulting from a single adaptive trend. Cranial specializations of comparable magnitude have occurred in other pinniped lineages, such as the remodelling of the front end of the skull resulting in a narial platform, weakly rooted cheek teeth, and mortised squamosal–jugal contact found in the unrelated but convergent *Mirounga angustirostris* and to some extent in *Hydrurga leptonyx* vs. *Allodesmus kelloggi*.

Is it not possible that odobenines (in the sense defined below) are more generalized than Otariini, perhaps to the degree that the common ancestor was more walrus-like than sea lion-like? If this were not the case, some lineages evidently underwent complete reversal of evolutionary trends, as in the development of the deltoid tuberosity. The deltoid tuberosity is primitively found within many groups of mammals, decidedly so within carnivores, the probable ancestors of pinnipeds. If Otariini gave rise to odobenines (known Otariini have the deltoid tuberosity incorporated into the deltoid crest), the position of the tuberosity would have been reversed in the lineage: primitive carnivore–Otariini–Odobeninae. It is much simpler to assume that the pinniped ancestor was odobenid-like in this feature. I intend to examine this question in detail in another essay, but here wish to re-emphasize the possibility that *O. rosmarus* is probably the closest living descendent of desmatophocines.

Desmatophoca oregonensis represents the earliest undoubted otariid pinniped yet described from the North Pacific (Condon, 1906), and is much more generalized than *Allodesmus* (Mitchell, 1966a). Although a detailed description and interpretation of the ventral surface of the skull has not yet been published, information from the dentition and dorsum of the skull (Condon, 1906; Mitchell, 1966a) suggests that the species can be regarded as a suitable sea lion ancestor in many ways. It is sea-lion like (Mitchell, 1966b, fig. 6 for restoration), and, with *D. oregonensis* and *A. kelloggi* probably contemporaneous in the middle Miocene, it is clear that a common ancestor for both species might be expected in the early Miocene or late Oligocene. This, as yet unknown, common ancestor might serve as a better species from which to derive all otariid types, but for the moment I shall consider *D. oregonensis* as sufficiently old enough and generalized enough to represent an approximation of the otariid ancestral type. There are problems in deriving both Otariini and Arctocephalini along with other otariids from a species like *D. oregonensis*, and it may be that the common ancestor necessary to link these groups is pre-middle Miocene. With this qualification in mind, a phylogeny can now be constructed as a first approximation of otariid relationships.

In an earlier work (1966a) I grouped *Desmatophoca*, *Allodesmus*, and *Dusignathus* within a subfamily Desmatophocinae. My present opinion is that, viewed across the spectrum of otariid genera, the Desmatophocinae are certainly distinct and might best be described as archaic otariids, but that *Allodesmus* (and perhaps *Dusignathus*) stand out even from this grouping and deserve at least subfamilial status (see below). Condon (1906) judiciously emphasized the resemblances of *Desmatophoca* to modern Otariini, and Kellogg (1931) just as judiciously pointed out the differences between all other pinnipeds and *Allodesmus* by erecting the family Allodesmidae.

Allodesmus kelloggi, known from better fossils than other allodesmine species, is markedly different from other otariids. It represents a specialization of the Otariidae convergent on some species of the Phocidae, for example in having a rostral platform like that found in *Mirounga*, a general skull shape like that in *Hydrurga*, weakly rooted postcanine teeth with smooth crowns like those in *Cystophora* and, *Mirounga*, and so on. The absence of supraorbital processes in early otariids like *Desmatophoca* and *Allodesmus* and in living *O. rosmarus* is a primitive, generalized feature retained, but it enhances the resemblance to phocids. Species of *Allodesmus* were so specialized that a phocid-like articulation between squamosal and jugal was evolved, and the zygomatic process of the squamosal was greatly enlarged and deepened. This situation, puzzling to Downs (1956), is probably related to the mode of feeding and attendant skull and jaw adaptation. These and other resemblances to phocids affirm the isolated position of *Allodesmus*, which was so specialized that it could not have given rise to any living otariid (Mitchell, 1966a). It evidently represents a group, specialized in habitus, that trended off from the mainline of otariid evolution and became extinct.

Dusignathus santacruzensis represents a structural grade through which the ancestral odobenid must have passed before the stage represented by *Prorosmarus* was reached (Mitchell, 1966a). This stage is characterized by reduced number of postcanine teeth with a loss of PC/6, increase in diameter of remaining cheek teeth, decrease in amount of enamel present on all teeth, development of long and slender upper canines, shortening of the mandible, and development of a pronounced genial tuberosity with an elongate symphysis that is not ankylosed. However, *D. santacruzensis* represents a parallel line, not within the ancestry of *Odobenus rosmarus* and its relatives, simply because it emphasized the lower canines as tusk-like structures and because it occurs well up into the Pliocene, much later than *Prorosmarus alleni*. *Prorosmarus alleni* shows reduction of the lower canine, as in species of *Alachtherium*, and can be broadly considered on the line leading to *O. rosmarus*. Thus *D. santacruzensis* is a sea lion and not a kind of true walrus. Walruses are a different kind of sea lion, distinct enough because of a separate history, possibly in a different ocean basin, to be given familial recognition for many years within the Pinnipedia. Now, with the discovery that there were many kinds of sea lions, some walrus-like but not walruses, others like living sea lions but not strictly the same lineage of species, and others that were quite different from any living otariid, it follows that all these must be accorded familial recognition if they are as distinct from living sea lions as are living walruses. Rejecting this as unreasonable splitting within Carnivora, I suggest instead that these major groups, represented by one or more species of comparable distinctness but all admittedly related to early otariids, be given subfamilial rank.

The familial disposition of *Pliopedia pacifica* Kellogg, 1921, poses a problem. The skull is unknown. Characters distinctly odobenine (especially the conformation of ulnar and radial fragments, and presence of a shallow depression on dorsal, proximal surface of metacarpal I) were weighed by Kellogg against other characters of an otariine nature and he tentatively referred the species to the Otariinae. No new material has been found, the holotype is evidently lost or misplaced, and reference has not generally been made to this taxon by other investigators. King (1964) followed Kellogg in listing it as an otariid, but Mitchell (1962, 1966a) considered it to be an odobenid. Dr Kellogg has graciously loaned to me the original illustrations, and perusal of these confirm my belief that a fossil odobenine, or at least nonotariine, is represented. *Pliopedia pacifica* may yet be found to represent some other type of desmatophocine descendent, and although I emphasize its odobenine affinities, its position is uncertain to some degree.

Valenictus imperialensis is evidently a specialized type of otariid that is distantly related to odobenines. Based upon a single humerus, the species is certainly distinct from any previously described (Mitchell, 1961) but its relationships are obscure. To place it within the Odobeninae, in the restricted sense that I use the term herein, would make a trash-basket group. It is obviously not on the lineage leading to *O. rosmarus*, but might be related to other, walrus-like sea lions such as *D. santacruzensis*, and possibly to *P. pacifica*. This is one of the least known areas of otariid evolution.

Neotherium mirum Kellogg, 1931 is an aquatic carnivore known from a few postcranial bones, and the phyletic relationship of the species is in doubt. Downs (1956) questioned the validity of the taxon, Mitchell (1961) tentatively referred a humerus to the species, and remarked (1966a) that the taxon represented a distinct, valid species and genus but that it was for the moment *incertae sedis*. The species is dealt with in another study by Mitchell and Tedford, and I have here omitted it from the phylogenetic chart.

As discussed above, the phyletic relationships of the species *Pontolis magnus* are also uncertain. Until the holotypic braincase can be prepared and restudied in detail, I must depend upon information derived from surficial features and from specimens possibly referable to the genus. As pointed out, there are a number of features in which *P. magnus* may resemble *I. downsi*, and I refer it to Imagotariinae or Odobeninae, *incertae sedis* until more information on *P. magnus* is forthcoming. *Pontolis magnus* is like living sea lions in some ways, such that True (1909) considered it as a direct ancestor of *Eumetopias jubata*. But it retains many features of the desmatophocines, and these serve to unite it on the one hand with *I. downsi* and on the other with *D. santacruzensis* (which also retains desmatophocine characteristics) and with Odobeninae.

Oriensarctos watasei is not placed upon the phylogenetic diagram (Fig. 16) because its relationships are uncertain. It might be a species of *Pontolis* but this is unlikely since I have shown in this paper that at least one specimen similar to *P. magnus* is related to *I. downsi*, and True originally assigned *P. magnus* to a position closely allied with living sea lions. *Oriensarctos watasei*, on the other hand, might represent a lineage of otariids with large, round cheek teeth comparable in some ways to *Dusignathus santacruzensis*. If the lower jaw (UOMNH 1938) and upper jaw (UW 2730) mentioned above prove referable to *Pontolis magnus*, then *Oriensarctos watasei* is distinct in having a long snout and three upper incisors vs. a shorter snout and two upper incisors.

Imagotaria downsi is an otariid that attained the sea lion grade of organization but did not give rise to living sea lions. Part of a lineage parallel to the Otariinae, and likely derived from a source more closely allied with true Desmatophocinae, *I. downsi* evidently became extinct and left no direct ancestors. It seems clear that derivation of a continuous paroccipital–mastoid wing is a specialization found in advanced otariids and is derived from the generalized condition of separate paroccipital and mastoid processes found in primitive species. It is a specialization in advanced otariids, and its presence is necessary in a true otariine. Since *I. downsi* has a small foramen lacerum posterius, a flat smooth bulla, and the tentorium appressed to the eminence for the semicircular canals, it is not otariine, but because it lacks separate mastoid and paroccipital processes, an inflated bulla, and a small membrana tympanica, it is not desmatophocine (sensu Mitchell, 1966a and below). As it does not exactly fall on the structural line from *D. oregonensis* to the Otariinae (because for one example, the lingual cingular cusps are greatly

emphasized; and confer the major divergent specializations in the ear region), it probably represents a phyletic offshoot. I propose the new subfamily Imagotariinae, characterized below with the type genus *Imagotaria*, to receive *I. downsi*. *Pontolis magnus* is related because the holotype shows some features like those found in *I. downsi*: the auditory bullae were relatively smooth and flat, and there was a smooth raised ridge along the posteroexternal edge of the bulla, probably associated with a groove between foramen stylomastoideum and vagina processus styloidei.

The adaptive radiation of the Arctocephalini must have been very complicated, as the taxonomic state of some living species and subspecies is in a state of flux and not yet well stabilized (e.g. see King, 1954; Sivertsen, 1954; Scheffer, 1958; and King, 1964; for some examples). The determination of generalized and specialized characters within the Otariinae still awaits definitive fossil evidence, the taxonomy of the subfamily is debated, the number of living genera and species has not yet been agreed upon (Sivertsen, 1953; Scheffer, 1958; King, 1960; Mitchell, 1966a). It would be unrealistic to attempt a definition of otariine structural stages (in terms of living species) exemplifying late Cenozoic radiation from a dispersal center, in the light of this uncertainty.

Pithanotaria starri was compared by Kellogg (1925a) only with a juvenile skeleton of *Callorhinus ursinus*, and he remarked that there were many resemblances. But it is possible that this fossil species could be more validly grouped with other nominal species of *Arctocephalus*. According to Kellogg's study the species *P. starri* is referable to Arctocephalini, and thus the earliest representative of this group. Presumably the split between Arctocephalini and Otariini, admittedly closely related taxa, took place before the end of the Miocene. If this is the case, then imagotariines, Otariini, Arctocephalini, dusignathines, and possibly other types of otariids inhabited late Miocene seas in the North Pacific.

I emphasize that within the Otariidae as I have now defined it, odobenines are about as different from otariines as desmatophocines are from allodesmines and dusignathines are from imagotariines.

To summarize: the Desmatophocinae were primitive sea lions aquatically adapted but retaining many generalized features. The Allodesminae represent a group derived from desmatophocines or possibly pre-desmatophocines that became specialized along phocid lines; descendents of some desmatophocines became benthonic feeders incorporating the lower canine into a crushing battery, the Odobeninae; other desmatophocines retained the lower canines but paralleled the odobenines, the Dusignathinae; some desmatophocines continued in a sea lion habitus and became specialized in their dentition and ear region, the Imagotariinae; other desmatophocines, paralleling imagotariines but with different specializations, possibly gave rise to the lineage of Otariinae; Arctocephalini was probably derived from or with early Otariini. Arctocephalini and Otariini are more similar to each other than either is to any subfamily: they should be grouped as tribes of Otariinae.

Two major segments of otariid evolution are almost completely unknown. The origin from terrestrial ancestors is not documented, and the later Miocene history involving origin or radiation of many otariid adaptive types is only suspected and inferred.

Such evidence as can be marshalled at the moment indicates that the Otariidae underwent a broad adaptive radiation before the late Miocene, expanding into a variety of marine habitats in the North Pacific Ocean. Some of these adaptive types became extinct, for reasons unknown, and at present at least one of these "morphotypes" is occupied by a phocid representative. This example, that of the convergence in form between the Miocene otariid *Allodesmus kelloggi* and the phocids *Mirounga* and *Hydrurga*, will be examined in detail in another study emphasizing the middle ear of allodesmines.

Some comments on relationships of the various species based on gross features of the skull and dentition have been made above. I here introduce a phylogeny of otariid pinnipeds, based mainly on the above evidence, published accounts, and work in progress. It can be regarded only as a first approximation, as some of the taxa are known from only one bone or fragments of a skull (e.g. *V. imperialensis*, *D. santacruzensis*, *P. magnus*, etc.) and most are known from only the skeleton of one individual. Pinniped phylogeny can best be documented by a series of morphologically graded fossils collected in the correct temporal sequence from a column of rocks. The present attempt to synthesize some of the existing data has resulted in one important conclusion: we have not yet collected enough fossils to give more than a first approximation of prehistoric events.

OTARIID SUBFAMILIES

Desmatophoca oregonensis is a generalized sea lion best regarded as distinct from living species at the subfamily level (Hay, 1930; Mitchell, 1966a). *Allodesmus kernensis*, *A. kelloggi*, and *A. courseni* are closely related one to another, and as a group more closely related to *D. oregonensis* than to living Otariini and Arctocephalini (Mitchell, 1966a). Kellogg (1931) proposed the new family Allodesmidae to emphasize the distinctness of *A. kernensis*, Camp and VanderHoof (1940) suppressed the family, Simpson (1945) did not recognize the family but commented that it might be a good subfamily if the entire family were consistently divided, and Mitchell (1966a) included *Allodesmus* and *Dusignathus* in the Desmatophocinae in order to emphasize the broad phyletic affinities of the genera.

From continuing studies on fossil pinnipeds, it is clear to me that a compromise should be derived between Kellogg's (1931) recognition of the Allodesmidae (including *Neotherium mirum*?) and my (Mitchell, 1966a) recognition of *Allodesmus* as a desmatophocine. The arrangement below recognizes the Desmatophocinae, Dusignathinae, Odobeninae, Allodesminae, Imagotariinae, and Otariinae.

The odobenines, fitted within Otariidae as a subfamily, are comparable with other subfamilies of carnivores in at least the development of enlarged

canines associated with a specialized mode of feeding. Examples such as Machairodontinae and Nimravinae within Felidae, and Thylacosmilinae within Borhyaenidae, readily come to mind and demonstrate that structural peculiarities related to different feeding mechanisms (Hough, 1950) have not been allowed to override basic familial relationships (Simpson, 1945) in taxonomic considerations.

Indeed, the spectrum now known within Otariidae, including odobenines, is more comparable with that already recognized within the Phocidae.

The anatomical features used in diagnosing the otariid subfamilies below are mostly basicranial structures, with other characters used where pertinent (see Table V). Most of the terminology is explained in this paper, but detailed descriptions, comparisons and diagnoses of Desmatophocinae, Allodesminae, and Dusignathinae will be forthcoming in additional studies in the series on extinct pinnipeds already begun (Mitchell, 1961, 1962, 1966a). Scheffer (1958, p. 135–149) has constructed a useful synoptic key to pinniped genera that effectively diagnoses Otariini and Arctocephalini and Odobeninae on other features.

Osteological resemblances between living sea lions and fur seals have prompted the lumping of Otariini and Arctocephalini under a single subfamily Otariinae. Such a move is all the more compelling because viable offspring are known from matings between *Zalophus californianus* and *Arctocephalus pusillus* (Schliemann, 1968; and see Scheffer, 1958 for mention of other hybrids). Is this proper between members of putative subfamilies of mammals? Within the overview of Otariidae, the Arctocephalini represent the most compact and mutually similar group of species, and I suspect that with more detailed study some of the genera might be lumped to advantage.

The subfamily Odobeninae is diagnosed upon the characters as known from *O. rosmarus*: detailed examination of species of *Alachtherium* and *Trichecodon* might serve to modify some of the critical features. Within the above subfamilies as diagnosed, I would include the genera and subgenera listed below. Some new terms have been introduced to make the classification consistent and to aid in presentation of my weighting of phyletic affinities of the taxa, but only within the Otariinae have tribes been introduced.

DESMATOPHOCINAE

Supraorbital process reduced or absent; sagittal crest reduced or absent; *squamosal appressed to dorsal surface of jugal in simple squamous contact*; nasals extend farther back than maxillaries on top of skull; mandibular symphysis not fused in adult; palate relatively flat; upper dentition 3I, 1C, 5+PC, lower dentition I1+?, 1C, 5+PC; PC2/-PC5/+? double rooted, PC/2-PC/5+? double rooted; upper and lower canines not greatly elongated, caniniform; heavy enamel on canines; lower canine not incorporated into crushing cheek tooth row; postcanine crowns with small lingual cingulum, major cingular cusp reduced to absent; *paroccipital process directed posteriorly*; *paroccipital process of exoccipital distinctly separated from mastoid process of squamosal, the two not fused or broadly continuous*; postglenoid foramen small; auditory bulla smooth, slightly inflated; apical bullar spur and fossa absent; inframeatal rim not spinose, smooth; *foramen stylomastoideum between ectotympanic and mastoid process*; *vagina processus styloidei present, posterolateral to bulla, not connected with foramen stylomastoideum via groove*; *posterior bullar*

projection absent; basioccipital not contributing to wall of canalis caroticus posteromedially; foramen caroticus posterius distinctly separate from foramen lacerum posterius; *foramen lacerum posterius medium size*; auditory cavity long, narrow and deep; hypotympanicum medium size, inflated anteriorly and laterally well beyond promontorium, *with small eminentia vagina processus styloidei on posteroexternal wall*; recessus meatus acousticus externi absent; *crista tympani not projecting into auditory cavity*; bulge of canalis caroticus touching promontorium, underlain by hypotympanicum slightly; *membrana tympanica almost round*, oriented slightly ventroexternally; promontorium globous, hanging in marked relief from dorsal wall of auditory cavity, inflated mainly posteriorly; fenestra cochleae medium to small.

ODOBENINAE

Supraorbital process reduced or absent; sagittal crest reduced or absent; *squamosal appressed to posterodorsal surface of jugal in simple squamous contact*; nasals extend farther back than maxillaries on top of skull; mandibular symphysis fused in adult; palate arched; upper dentition I1 ?, C1, PC4 ?+, lower dentition I0, C1, PC3+ ?; all teeth single rooted; no pronounced cingular cusps or cingulum, crowns wear with age; *upper canines greatly enlarged, tusk like*; enamel reduced to absent; *lower canine with tendency to be incorporated into crushing cheektooth row*; *paroccipital process of exoccipital thin, plate like, appressed to back end of paroccipital–mastoid flange*; *paroccipital and mastoid processes continuous, massive, directed ventrally*; postglenoid foramen medium size; auditory bulla flat, wrinkled; apical bullar spur and fossa small to absent; inframeatal rim spinose, major spine situated far dorsoposteriorly; *foramen stylomastoideum between ectotympanic and mastoid process*; *vagina processus styloidei present, small, posteroexternal to bulla, connected with foramen stylomastoideum via groove between bulla and mastoid*; *posterior bullar projection absent, labrum vagina processus styloidei absent*; basioccipital may contribute to wall of canalis caroticus; foramen caroticus posterius separate from foramen lacerum posterius; *foramen lacerum posterius medium size*; auditory cavity long, narrow, and deep, mastoid may contribute to wall internal to eminentia vagina processus styloidei; hypotympanicum large, inflated posteriorly, ventral and anterior to promontorium, *with small eminentia vagina processus styloidei on posterior wall*; recessus meatus acousticus externi small to absent; *crista tympani projected into auditory cavity, without overhanging, free edge ventrally*; bulge of canalis caroticus almost touching promontorium, not underlain by hypotympanicum posteriorly; tympanohyal enclosed within vagina processus styloidei at level of membrana tympanica, contacts and may fuse with pars petrosa in or near wall of facial canal; *membrana tympanica almost round, oriented ventrointernally*; recessus epitympanicus pear shaped, well defined, with wide fossa incudis; septum canalis musculotubarii a simple bony shelf, not touching roof of auditory cavity; promontorium low, broad, inflated only posteriorly, bears major flange on posteroexternal edge; fenestra cochleae wide; pars petrosa excavated for canalis petrobasilaris; tympanic wall of canalis caroticus may contribute to wall of canalis petrobasilaris; pars petrosa dorsal to meatus acousticus internus flattened, slightly striated, defined from ventral part by flange; *fossa cerebellaris deeper than transverse width of entrance*; *tentorium appressed to eminence containing semicircular canals*.

DUSIGNATHINAE

Sagittal crest reduced, *squamosal appressed to dorsal surface of jugal in simple squamous contact*; mandibular symphysis not fused in adult; genial tuberosity pronounced; palate slightly arched; lower dentition I ?, C1, PC5; postcanines haplodont, closely spaced, single rooted, with large, deep roots; PC/5 present, large; *upper canine not greatly elongated, moderately tusk like*, apical foramen closes with increased age; enamel present on canines but reduced (?); *lower canine not premolariform and not incorporated into crushing postcanine tooth row, moderately tusk like*; *paroccipital process continuous with mastoid process*; postglenoid process reduced, mandibular condyle bearing mainly dorsally into glenoid fossa; *stylomastoid foramen not continuous via a groove with vagina processus styloidei*; *vagina processus styloidei near posterior end of bulla, opening into auditory cavity*; hypotympanicum not greatly inflated; surface of bulla relatively smooth and flat; *eminentia vagina processus styloidei small to absent*; recessus meatus acousticus externi

small; *crista tympani slightly projected into auditory cavity, without overhanging, free ventral edge*; *membrana tympanica subquadrate in shape, longest side dorsoventrally oriented*, slanting anteroventrointernally about 60° from axis meatus acousticus externus; recessus epitympanicus well delineated, with medium to narrow fossa incudis.

ALLODESMINAE

Supraorbital process reduced or absent; sagittal crest reduced or absent; *squamosal appressed to jugal in mortise-like manner*; nasals extend farther back than maxillaries on top of skull; mandibular symphysis not fused in adult; palate arched; upper dentition I3, C1, PC6, lower dentition I2, C1, PC6; all postcanines single rooted; PC5/-PC6/ reduced in size; PC/4-PC/5 diastema sometimes present; postcanine crowns with no major cingular cusps, cingulum reduced to absent, crowns inflated and smooth; upper and lower canines not greatly elongated, caniniform; heavy enamel on canines; lower canine not incorporated into crushing cheektooth row; *paroccipital process of exoccipital contributes one half or more to formation of paroccipital process, not thin and plate like*; *paroccipital process discrete, directed posteroexternally, not broadly continuous with mastoid process*; postglenoid foramen small; auditory bulla flat and wrinkled; apical bullar spur and fossa absent; inframeatal rim wrinkled; *foramen stylomastoideum nearly behind bulla, not directly between bulla and mastoid process*; *vagina processus styloidei present, large, shallow, almost posterior to bulla, not connected with foramen stylomastoideum via a groove around bulla*; *posterior bullar projection absent*; *labrum vagina processus styloidei absent*; basioccipital does not contribute to wall of canalis caroticus posteriorly; foramen caroticus posterius separate from foramen lacerum posterius; *foramen lacerum posterius small*; auditory cavity long, deep, bowed externally; mastoid evidently does not contribute to wall internal to eminentia vagina processus styloidei; hypotympanicum large, inflated externally and ventrally well beyond promontorium, *with eminentia vagina processus styloidei small to absent on posterior wall*; recessus meatus acousticus externi small to absent; *crista tympani not projected into auditory cavity, without overhanging free ventral edge*; bulge of canalis caroticus vascularized, appressed to promontorium, not underlain by hypotympanicum extensively; tympanohyal enclosed within vagina processus styloidei at level of membrana tympanica or lower, exposed on wall of auditory cavity; *membrana tympanica almost round, oriented almost vertically*; recessus epitympanicus large, globous, not well delineated from rest of tympanic cavity, with wide fossa incudis; septum canalis musculotubarii reduced to absent; promontorium hanging far into auditory cavity, globous, inflated mainly posteriorly; pars petrosa not markedly excavated for canalis petrobasilaris; tympanic wall of canalis caroticus does not contribute to wall of canalis petrobasilaris; pars petrosa dorsal to meatus acousticus internus flattened, striated slightly, defined from ventral part indistinctly by ridge; *fossa cerebellaris deeper than transverse width of entrance*; *tentorium appressed to eminence containing semicircular canals*.

IMAGOTARIINAE

Palate arched; upper dentition 3I, 1C, 5+PC, lower dentition 2I, 1C, 6PC; most postcanines incipiently double rooted; postcanine crowns with enlarged lingual, cingular cusps; upper and lower canines not greatly elongated, caniniform; heavy enamel on canines; lower canines not incorporated into crushing cheektooth row; *paroccipital thin, plate like*; *paroccipital and mastoid processes broadly continuous, directed ventrally*; postglenoid foramen large; auditory bulla smooth and flat; apical bullar spur and fossa present; inframeatal rim spinose; *foramen stylomastoideum between ectotympanic and mastoid process*; *vagina processus styloidei present, large, directly posterior to bulla, connected with foramen stylomastoideum via groove behind bulla*; *posterior bullar projection present*; *labrum vagina processus styloidei present*; basioccipital contributing to wall of canalis caroticus posteromedially, which is otherwise enclosed in entotympanic; foramen caroticus posterius separate from foramen lacerum posterius; *foramen lacerum posterius small*; sphenoid contributing to canalis caroticus internus wall; auditory cavity long, narrow, deep, mastoid does not contribute to wall internal to eminentia vagina processus styloidei; hypotympanicum large, inflated medially and ventrally well beyond promontorium, *with pronounced eminentia vagina processus styloidei on posterior wall*; recessus meatus acousticus externi small; *crista*

tympani projected into auditory cavity, without overhanging, free ventral edge; bulge of canalis caroticus almost touching promontorium, underlain by hypotympanicum posteriorly; tympanohyal enclosed within vagina processus styloidei at level of membrana tympanica; *membrana tympanica almost round, longest diameter anteroposteriorly*, oriented ventrointernally 60° from axis meatus acousticus externus; recessus epitympanicus pear shaped, well delineated, with narrow fossa incudis; septum canalis musculotubarii a cylindrical shell almost touching dorsal roof of auditory cavity; promontorium low, inflated only posteriorly; fenestra cochleae huge; groove on promontorium ventral to fenestra vestibuli; nervus vagus ramus auricularis passes dorsoposterior to tip of tympanohyal; pars petrosa not excavated for canalis petrobasilaris; tympanic wall of canalis caroticus may not contribute to wall of canalis petrobasilaris; pars petrosa dorsal to meatus acousticus internus flattened, striated slightly, defined from ventral part by sulcus; *fossa cerebellaris deeper than transverse width of entrance*; *tentorium appressed to eminence containing semicircular canals.*

OTARIINAE

Supraorbital process present, often strong; sagittal crest present, to strongly developed; *squamosal appressed to dorsal surface of jugal in simple squamous contact*; nasals extend farther back than maxillaries on top of skull; mandibular symphysis not fused in adult; palate flat to arched; upper dentition 3I, 1C, 5-6PC, lower dentition 2I, 1C, 5PC; postcanine teeth single to double rooted; postcanine crowns with lingual cingulum, often with small cingular cuspules, no single major cingular cusp; upper and lower canines not greatly elongated, caniniform; heavy enamel on canines; lower canine not incorporated into crushing cheek tooth row; *paroccipital thin, plate like*; *paroccipital and mastoid process broadly continuous, directed ventrally or posteroventrally*; postglenoid foramen small; ventral surface of bulla usually roughened, with strong projections (often smooth and flat in Arctocephalini); back edge of bulla stands markedly down from basicranial surface with great relief; apical bullar spur and fossa absent; *foramen stylomastoideum between bulla and mastoid process*; *vagina processus styloidei present but variable, shallow, small to medium size, posteroexternal to bulla, not connected with foramen stylomastoideum by a distinct groove*; *posterior bullar projection absent*; *labrum vagina processus styloidei absent*; basioccipital usually does not contribute to internal lip of foramen caroticum posterius in Otariini, does in Arctocephalini; foramen caroticus posterius opens toward foramen lacerum posterius; *foramen lacerum posterius a large vacuity*; sphenoid contributes to canalis caroticus internus wall; auditory cavity long, narrow, relatively deep; mastoid may not contribute to wall internal to eminentia vagina processus styloidei; hypotympanicum large, inflated medially, posteriorly, and ventrally well beyond promontorium, *with small eminentia vagina processus styloidei on posterior wall*; recessus meatus acousticus externi small to medium size; *crista tympani projected into auditory cavity, may have overhanging, free ventral edge*; bulge of canalis caroticus touches promontorium, underlain by hypotympanicum posteriorly; tympanohyal enclosed within vagina processus styloidei at or below level of membrana tympanica; *membrana tympanica generally ovate, with long axis dorsoventrally*, oriented ventrointernally; recessus epitympanicus pear shaped, well delineated, relatively small, with narrow fossa incudis; fossa incudis does not usually extend back beyond level of posteroexternal corner of promontorium; septum canalis musculotubarii a thin, bony shelf not touching dorsal roof of auditory chamber; promontorium low, not hanging far down within auditory chamber, inflated anteriorly and posteriorly; fenestra cochleae medium to large; groove on promontorium ventral to fenestra vestibuli; pars petrosa excavated for canalis petrobasilaris; tympanic wall of canalis caroticus contributes to wall of canalis petrobasilaris; pars petrosa dorsal to meatus acousticus internus rounded, smooth, not well defined from ventral part; *fossa cerebellaris not deeper than transverse width of entrance*; *tentorium not appressed to eminence containing semicircular canals.*

PROVISIONAL OTARIID CLASSIFICATION

Family OTARIIDAE *sensu lato*
- Subfamily DESMATOPHOCINAE
  - Genus *Desmatophoca* Hay, 1930
- Subfamily ODOBENINAE
  - Genus *Prorosmarus* Berry and Gregory, 1906
  - Genus *Alachtherium* Du Bus, 1867
  - Genus *Trichecodon* Lankester, 1865
  - Genus *Odobenus* Brisson, 1762
- ?ODOBENINAE or ?DUSIGNATHINAE, *incertae sedis*
  - Genus *Pliopedia* Kellogg, 1921
  - Genus *Valenictus* Mitchell, 1961
  - Genus *Oriensarctos* new genus
- Subfamily DUSIGNATHINAE
  - Genus *Dusignathus* Kellogg, 1927
- Subfamily ALLODESMINAE
  - Genus *Allodesmus* Kellogg, 1922
    - Subgenus *Allodesmus* (Kellogg, 1922)
    - Subgenus *Atopotarus* (Downs, 1956)
- ?IMAGOTARIINAE or ?ODOBENINAE, *incertae sedis*
  - Genus *Pontolis* True, 1905
- Subfamily IMAGOTARIINAE
  - Genus *Imagotaria* new genus
- Subfamily OTARIINAE *sensu lato*
  - Tribe Otariini
    - Genus *Phocarctos* Peters, 1866
    - Genus *Otaria* Peron, 1816
    - Genus *Zalophus* Gill, 1866
    - Genus *Neophoca* Gray, 1866
    - Genus *Eumetopias* Gill, 1866
  - Tribe Arctocephalini
    - Genus *Pithanotaria* Kellogg, 1925
    - Genus *Callorhinus* Gray, 1859
    - Genus *Arctocephalus* Geoffroy and Cuvier, 1826

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Influence of Temperature and Photoperiod on Guanine and Hypoxanthine Levels in Skin and Scales of Atlantic Salmon (*Salmo salar*) during Parr–Smolt Transformation[1,2]

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ABSTRACT

The influences of temperature and photoperiod on the purine (guanine, hypoxanthine) levels in skin and scale silvery layers of Atlantic salmon at parr–smolt transformation were assessed by holding 2-year-old parr from December to June under four controlled temperature and photoperiod regimes: NLNT, 8LNT, NL3T, and 8L3T (where NL = naturally lengthening daily photoperiod; 8L = 8-hr daily photoperiod; NT = temperature held at 3 ± 1 C until mid-March and then rising to 14 C in June; 3T = temperature maintained at 3 ± 1 C throughout).

From December through to March, levels of both purines increased under all four regimes. From April through to June purine levels continued to increase but were greater under NT than 8T regimes, showing that temperature influences purine deposition. Photoperiod changes did not modify purine levels appreciably. Other factors presumably influence silvering since under 8L3T (sustained "winter" conditions) purine levels more than doubled between December and June. The guanine/hypoxanthine ratio, higher for skin than for scale silvery layers, changed little seasonally and showed negligible dependence on temperature and photoperiod. Visual assessment of the extent of silvering correlated closely with measured purine levels. Increases in the fresh weight of fish were similar under all four regimes but a more pronounced decrease in the coefficient of condition occurred under NT regimes.

INTRODUCTION

The silvering in Atlantic salmon at parr–smolt transformation is produced by increased amounts of the crystalline purines guanine and hypoxanthine, both beneath the scales and in a second deep dermal layer (Johnston and Eales, 1967).

A correlation between rising water temperatures in spring and the increased purine levels during parr–smolt transformation was obtained for field and laboratory-held populations of 2-year-old Atlantic salmon (Johnston and Eales, 1967). However, with no control population the causal relationship between temperature and purine deposition was unknown, and the lengthening daily photoperiod in spring might exert some effect. In this study the influences of temperature and photoperiod on guanine and hypoxanthine levels in the scale and skin silvery layers of 2-year-old Atlantic salmon during parr–smolt transformation were investigated experimentally.

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MATERIALS AND METHODS

In November, 1000 2-year-old Atlantic salmon parr exceeding 10 cm fork length were obtained from the Miramichi Fish Culture Station, South Esk, N.B. They were divided randomly into four equal populations, each held in a grey rectangular plywood tank (236 × 45 × 56 cm). Ground liver (200 g) was fed per tank every 2 days.

Each tank was light-proof and had three 15-w daylight fluorescent bulbs fixed to a hinged lid so that the lights were about 8 cm above the water surface. In two tanks the daily photoperiod was set at 8 hr beginning on December 21 (8L), whereas in the other two tanks it was regulated by a photocell exposed to the sky and increased from 8 hr on December 21 to 15 hr in mid-June (NL) (Fig. 1).

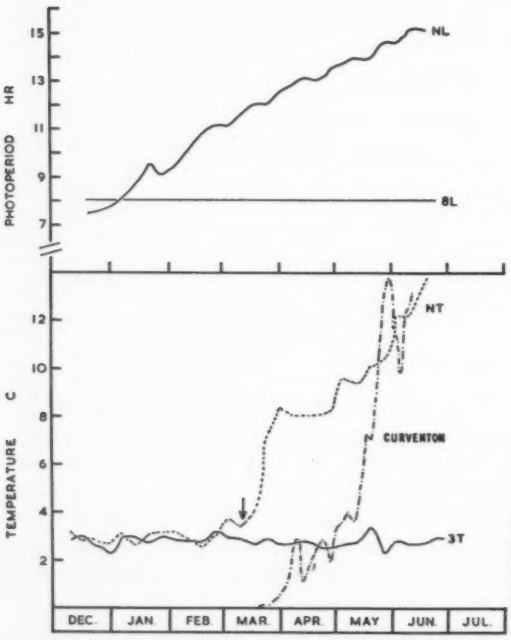

FIG. 1. Changes in daily photoperiod and temperature for the four regimes, and temperature record for the Northwest Miramichi River at Curventon in 1966. The arrow signifies the increase in temperature in NT regimes on March 12.

A steady flow of fresh temperature-controlled aerated water obtained from the Fredericton City reservoir was supplied to each tank. In two tanks the water temperature was maintained from December to late June at 3 ± 1 C (3T). In the other two tanks (NT) the water temperature was maintained at 3 ± 1 C until March 12. After March 12 the water temperature rose approximately 1 degree C every 3 days until 8 C was reached, and then rose more gradually to 14 C in late June (Fig. 1). The NT regime was supposed to simulate

field temperatures but, owing to the limitations of the refrigeration system, temperatures for nearby New Brunswick streams could not be duplicated exactly. The temperature records for the NT regime and for the Northwest Miramichi River at Curventon, New Brunswick, in 1966 are shown in Fig. 1.

The four temperature and photoperiod combinations used were:

Temp	Photoperiod	Code
3±1 C from December until March 12 and then increasing to 14 C by June	Lengthening from 8 hr in December to 15 hr in June	NLNT
	8 hr December to June	8LNT
3±1 C from December to June	Lengthening from 8 hr in December to 15 hr in June	NL3T
	8 hr December to June	8L3T

Guanine and hypoxanthine levels were measured at monthly intervals (except for February) for skin and scale silvery layers of 8–10 fish selected randomly from each of the four regimes. Since it took several days to extract purines from each group of fish for a given condition, all four groups could not be measured simultaneously. Samples were staggered, one group being examined each week of the month. The procedure for quantitative analysis of integumentary purines has been described by Johnston and Eales (1967).

RESULTS

Scale guanine and hypoxanthine levels increased steadily in all four regimes until March (Fig. 2, Table I). For 3T regimes this steady increase was maintained until June. However, for NT regimes, levels increased sharply as water temperatures rose, indicating an influence by temperature on purine deposition.

Manipulation of daily photoperiod had less influence on scale purine levels. For 3T regimes there was no difference between fish from 8L and NL regimes in late May, although in June NL levels slightly exceeded 8L levels. For NT regimes NL levels slightly exceeded 8L levels from December until May suggesting a possible photoperiod effect. However, the difference between purine levels from 8LNT and NLNT regimes in May, when there was a large difference in photoperiod, was not greater than the difference between purine levels from these regimes in December and January when there was little difference in photoperiod (Fig. 2). Furthermore, although both NLNT and 8LNT regimes were held at 3 ± 1 C until March 12, the NLNT fish received slightly warmer water than the 8LNT fish. Since temperature has already been shown to influence purine deposition, the small difference in purine

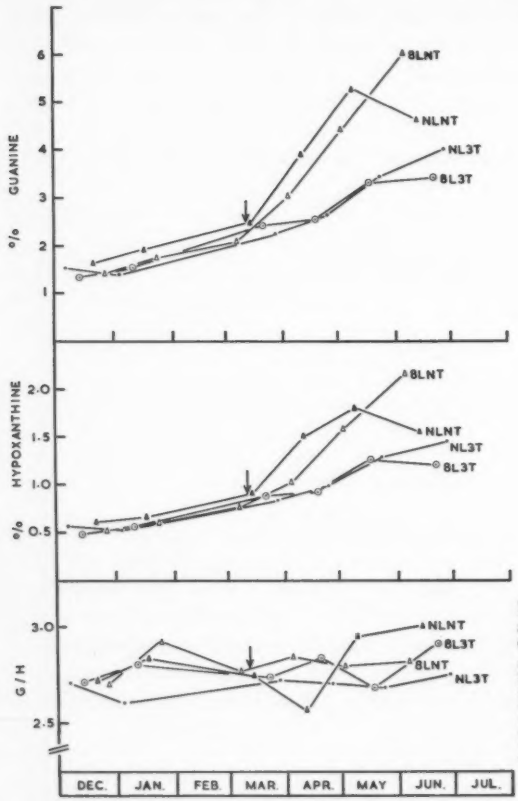

FIG. 2. Seasonal changes in guanine and hypoxanthine contents and in G/H ratio in the scale silvery layer of fish held under four different temperature and photoperiod regimes. Each point represents a mean for 8–10 fish. The arrow signifies the increase in temperature in NT regimes on March 12. Means and standard errors are given in Table I.

levels between 8LNT and NLNT regimes could result from the small temperature discrepancy between the two regimes.

In June purine levels in scales from NLNT regimes decreased. This decrease may represent a reabsorption of purines from fully silvered fish maintained in fresh water beyond the time of migration. However, the scales of smolts are lost easily on handling and loss also occurs without handling. The extent to which scale and purine loss may have influenced the scale purine measurements in smolts is not known. The NLNT fish were slightly more advanced throughout than 8LNT fish and may have been more susceptible to such effects.

Guanine and hypoxanthine levels for the skin silvery layer (Fig. 3, Table I) were considerably greater than those for the scale silvery layer. As for those in scales, purine levels in skin rose in 3T regimes from December until June and increased in NT regimes more markedly after than before the mid-March temperature rise. For 3T regimes there was little difference between

TABLE I. Guanine and hypoxanthine contents and G/H ratios in scale and skin silvery layers, along with size and condition, of fish held under four temperature and photoperiod regimes from December to June.

TABLE I. Guanine and hypoxanthine contents and G/H ratios in scale and skin silvery layers, along with size and condition, of fish held under four temperature and photoperiod regimes from December to June.

Sampling date	Regime	Fresh wt (g)		Fork length (cm)		Coeff. of condition		Scale silvery layer						Skin silvery layer					
								Guanine (%)		Hypoxanthine (%)		G/H		Guanine (%)		Hypoxanthine (%)		G/H	
		$\bar{X}$[a]	SE[b]	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Dec. 6–7	NL3T	20.6	1.008	12.7	0.212	1.00	0.006	1.57	0.104	0.58	0.045	2.72	0.055	5.03	0.247	1.30	0.077	3.90	0.134
13–14	8L3T	20.1[c]	0.970	12.5	0.260	1.04	0.021	1.33	0.077	0.49	0.032	2.73	0.063	5.10	0.251	1.34	0.055	3.80	0.077
21–22	NLNT	20.8	0.881	12.8	0.172	0.98	0.011	1.67	0.055	0.61	0.014	2.73	0.063	5.65	0.197	1.44	0.045	3.94	0.077
27–28	8LNT	17.8	1.186	12.2	0.254	0.97	0.017	1.41	0.055	0.53	0.089	2.71	0.095	5.21	0.243	1.34	0.063	3.85	0.122
Jan. 3–4	NL3T	18.6	1.141	12.4	0.254	0.97	0.025	1.40	0.089	0.53	0.032	2.61	0.055	5.94	0.263	1.49	0.055	3.98	0.063
10–11	8L3T	18.9	1.101	12.2	0.225	1.02	0.018	1.56	0.089	0.56	0.032	2.81	0.063	6.33	0.263	1.64	0.077	3.89	0.134
17–18	NLNT	19.0	1.239	12.7	0.230	0.92	0.017	1.91	0.084	0.67	0.032	2.84	0.045	7.79	0.281	1.90	0.077	4.11	0.045
24–25	8LNT	17.7	0.817	12.2	0.183	0.97	0.018	1.79	0.077	0.62	0.045	2.93	0.209	5.78	0.226	1.49	0.045	3.87	0.195
Mar. 7–8	8LNT	22.3	1.192	13.0	0.202	1.00	0.018	2.11	0.145	0.76	0.055	2.77	0.077	7.07	0.463	1.81	0.122	3.93	0.100
14–15	NLNT	23.2	1.142	13.2	0.179	0.99	0.022	2.49	0.138	0.90	0.045	2.75	0.045	7.49	0.329	1.87	0.100	4.00	0.089
21–22	8L3T	20.7	0.773	12.8	0.130	1.01	0.018	2.42	0.239	0.88	0.083	2.74	0.063	7.13	0.316	1.82	0.195	3.94	0.083
28–29	NL3T	22.3	0.744	13.0	0.147	1.01	0.015	2.29	0.095	0.84	0.032	2.73	0.045	6.95	0.443	1.72	0.084	4.02	0.104
Apr. 4–5	8LNT	23.2	1.344	13.4	0.230	0.95	0.023	3.07	0.084	1.04	0.077	2.84	0.063	8.60	0.355	2.09	0.089	4.13	0.118
11–12	NLNT	23.7[d]	1.669	13.7	0.331	0.91	0.015	3.89	0.261	1.51	0.030	2.57	0.077	7.86	0.454	2.18	0.134	3.63	0.149
18–19	8L3T	22.4	0.937	13.0	0.200	1.02	0.016	2.58	0.155	0.91	0.045	2.84	0.114	7.55	0.387	1.80	0.077	4.17	0.100
25–26	NL3T	24.3	0.800	13.5	0.148	0.98	0.026	2.69	0.202	0.99	0.055	2.71	0.089	7.87	0.253	1.93	0.077	4.08	0.077
May 3–4	8LNT	23.5	1.471	13.7	0.290	0.90	0.016	4.41	0.396	1.58	0.138	2.79	0.055	9.33	0.879	2.44	0.268	3.87	0.149
9–10	NLNT	24.5	1.226	14.4	0.285	0.82	0.011	5.29	0.192	1.80	0.077	2.95	0.055	10.16	0.300	2.51	0.077	4.04	0.055
17–18	8L3T	24.8	1.342	13.7	0.268	0.96	0.013	3.32	0.200	1.25	0.100	2.68	0.077	9.13	0.530	2.33	0.141	3.94	0.077
23–24	NL3T	28.0	1.955	14.2	0.327	0.96	0.026	3.44	0.197	1.28	0.077	2.68	0.045	10.38	0.237	2.61	0.077	3.98	0.063
June 6–7	8LNT	27.6	2.395	14.7	0.426	0.84	0.009	6.08	0.424	2.17	0.155	2.83	0.138	16.44	0.837	3.95	0.226	4.24	0.270
13–14	NLNT	29.5	0.825	15.7	0.109	0.76	0.047	4.63	0.365	1.54	0.110	3.03	0.148	12.57	0.563	3.00	0.170	4.24	0.152
21–22	8L3T	28.2	1.363	14.3	0.255	0.95	0.016	3.41	0.224	1.20	0.098	2.92	0.176	10.22	0.421	2.40	0.130	4.34	0.266
27–28	NL3T	30.4	1.785	14.8	0.265	0.93	0.016	4.02	0.283	1.45	0.077	2.75	0.095	10.72	0.200	2.91	0.141	3.70	0.182

[a] $\bar{X}$ = mean of value from 10 fish unless otherwise indicated.
[b] SE = ± standard error of mean.
[c] Sample size = nine fish.
[d] Sample size = eight fish.

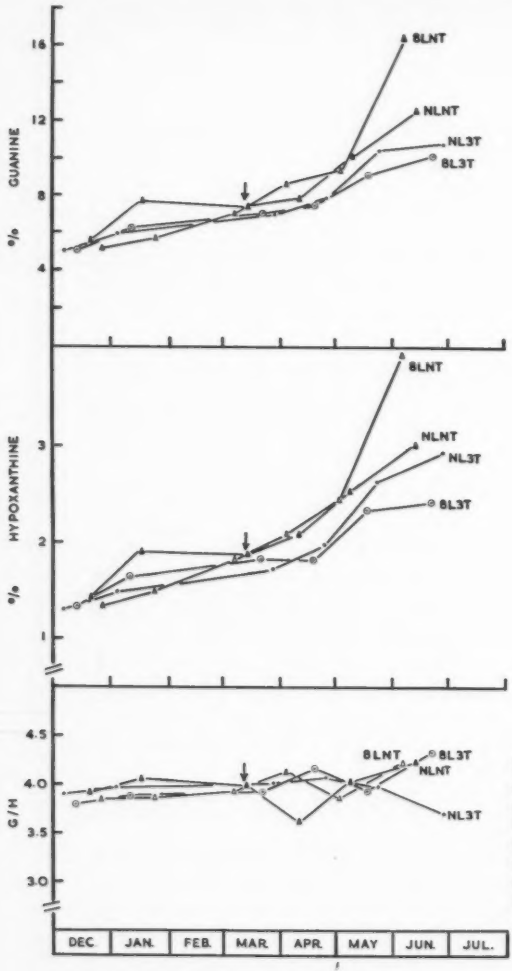

FIG. 3. Seasonal changes in guanine and hypoxanthine contents and in G/H ratio in the skin silvery layer of fish held under four different temperature and photoperiod regimes. Each point represents a mean for 8–10 fish. The arrow signifies the increase in temperature in NT regimes on March 12. Means and standard errors are given in Table I.

8L and NL skin purine levels although NL levels were slightly higher than 8L levels from late April until June. For NT regimes skin purine levels were higher in June for 8L than for NL. Prior to June the difference between skin purine levels for 8LNT and NLNT was slight. There is little evidence that for either 3T or NT regimes lengthening photoperiod was associated with increased purine deposition in the skin silvery layer.

Higher G/H (guanine/hypoxanthine) ratios were consistently found in the skin silvery layer than in the scale silvery layer (Fig. 2 and 3, Table I). For both layers there was little seasonal change in the G/H ratio and negligible influence by temperature and photoperiod manipulation. The

general constancy of skin and of scale G/H ratios suggests a close parallel between the factors determining guanine and hypoxanthine deposition in either skin or scale silvery layers.

The fish for which purines were measured were classified immediately before death as parr, smolt, and silvery parr (Table II). The visually assessed

TABLE II. Visual assessment of extent of smoltification in fish for which purine levels were measured.

	NLNT			8LNT			NL3T			8L3T		
	P[a]	SP	S	P	SP	S	P	SP	S	P	SP	S
Dec.	–	10	–	–	10	–	3	7	–	3	6	–
Jan.	–	10	–	–	10	–	–	10	–	–	10	–
Mar.	–	10	–	–	10	–	–	10	–	–	10	–
Apr.	–	2	6	–	10	–	–	10	–	–	10	–
May	–	2	8	–	5	5	–	10	–	–	9	1
June	–	2	8	–	1	9	–	10	–	–	10	–

[a]P = parr (yellowish sides and fins, dark parr marks and only slight ventral silvering); S = smolt (no visible parr marks, silvery instead of yellowish sides and black margins around fins); SP = silvery parr (a variable condition intermediate between parr and smolt).

state of smoltification was closely associated with the skin and scale purine levels. For 3T regimes only one smolt was recorded by June, whereas for NT regimes most fish were smolts by May or June. In April and May under NT regimes more smolts were recorded for NL than for 8L regimes. Under 3T regimes little influence by photoperiod was evident.

For each monthly sample the fresh weights and fork lengths were recorded (Fig. 4, Table I). There was little difference between fresh weights for the

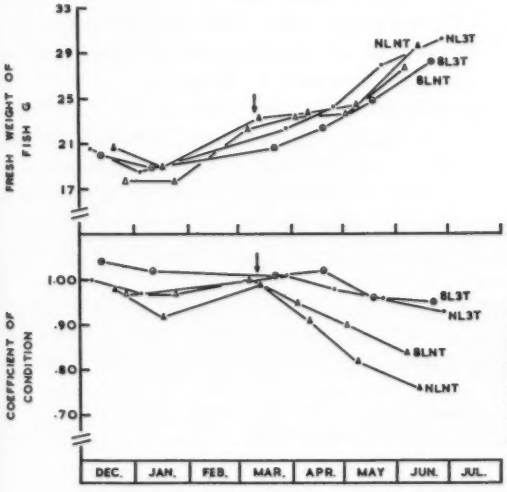

FIG. 4. Seasonal changes in fresh weight and coefficient of condition for fish held under four different temperature and photoperiod regimes. Each point represents the mean for 8–10 fish. The arrow signifies the increase in temperature in NT regimes on March 12. Means and standard errors are given in Table I.

four regimes, although under either 3T or NT conditions, NL fish generally had mean fresh weights slightly exceeding those for 8L fish. The data suggested no temperature influence on fresh weight.

The coefficient of condition[4] varied between the four regimes. For 3T regimes it decreased slightly but for NT regimes it decreased more rapidly, especially under NLNT.

In the present study fork length was used.

DISCUSSION

The present data indicate that the skin and scale silvering in Atlantic salmon smolts is not influenced appreciably by lengthening photoperiod but does depend on temperature. There are few other studies with which to compare these findings.

Unpublished results of experiments carried out in 1964 by the Fisheries Research Board of Canada (1966, p. 33) indicate a combined influence of temperature and photoperiod on changes in guanine deposition and coefficient of condition at parr–smolt transformation of coho salmon. Yearlings held at 8.5 C with a 16-hr day, with an increasing photoperiod and with an 8-hr day smoltified in late February, March, and early May respectively. Another group held at a lower temperature showed little change in the coefficient of condition under any of the above three photoperiod regimes, although the guanine levels were elevated slightly by the end of the experiment.

Van Overbeeke (Hoar, 1965) held yearling coho parr under four temperature and photoperiod regimes comparable with those used in the present study. In late July he observed the greatest incidence of smolts in the population held under conditions of naturally increasing temperature and lengthening photoperiod, whereas the lowest incidence of smolts at this time occurred at low temperatures and under a constant 8-hr photoperiod. However, by late summer the regime of low temperature and short photoperiod had a high percentage of silvery smolts. This suggests that although manipulation of environmental variables may postpone or accelerate smoltification in coho, their manipulation cannot eliminate the phenomenon altogether.

Baggerman (1960, 1962) demonstrated the importance of daily photoperiod on the development of salinity preference at parr–smolt transformation in coho. Eales (1965) showed that for 2-year-old parr of steelhead trout (*S. gairdneri*) the increase in thyroid activity characteristic of smolts depended upon both increasing temperature and lengthening photoperiod. Evidently generalization cannot be made between species concerning environmental control of the development of smolt features.

The present data also show an increase in skin and scale purine levels under sustained "winter" (8L3T) conditions. Since neither a temperature increase nor a change in photoperiod seems to be required to induce the onset

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[4]Coefficient of condition $= \frac{\text{wt of fish (g)} \times 100}{\text{total length (cm)}^3}$ (Hoar, 1939).

of silvering, other environmental variables or endogenous factors are involved. Elson (1954) has concluded that, as a rule-of-thumb guide, Atlantic salmon parr attaining approximately 10 cm (total length) by the end of their growing season in the fall would probably smoltify the following spring whereas those less than 10 cm would not. Possibly once Atlantic salmon acquire a certain size and physiological state silvering begins regardless of the environment, although the environment could modify the rate of the processes involved. Atlantic salmon in many New Brunswick streams are exposed to water at 0 C from December to April. During this period purine deposition may be taking place but be negligible at such low temperatures. Not until temperatures rise rapidly in spring would appreciable silvering occur. In NT regimes in the laboratory, silvering took place over several weeks. However, fish in nature exposed to a lower winter temperature but a sharper spring temperature increase would presumably silver more rapidly.

It is possible that all silvering changes are not necessarily related to parr–smolt transformation, but may represent a gradual adaptation to the photic conditions in the experimental tanks. Incident and background illumination would presumably differ from those previously experienced by the fish. Sumner (1944) held *Girella nigricans* on several backgrounds and observed up to a four-fold change in guanine levels over a 4-month period. A comparable adaptation to background could occur for Atlantic salmon under the present laboratory conditions.

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Two Methods of Describing the "Average" Vertical Temperature Distribution of a Lake[1,2]

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ABSTRACT

The "average" vertical temperature distribution of a stratified freshwater lake can be obtained from a series of samples by various techniques. Two of these are described: computation of the average temperature at different levels and computation of the average depth of a number of isotherms. It is concluded that the latter technique can, under certain conditions, give a more realistic approximation of the observed temperature profiles, especially in the thermocline region.

INTRODUCTION

From a descriptive point of view, it is often advantageous to reduce a large number of data to a series of average values, and to contrast the individual observations to these averages rather than comparing them with each other. In a study of the vast amount of water-temperature data gathered by the Great Lakes Division of the Department of Energy, Mines and Resources, the author examined various ways of reducing large numbers of bathythermograph data. Vertical temperature traces, henceforth called Temperature-Depth or T-D curves, can be reduced by three different methods.

A mean vertical temperature distribution can be obtained either by averaging the temperature at a number of standard depths or by averaging the depth of a number of isotherms. The first method, which is most commonly used, does not always give an average T-D curve that is representative for the individual observations. It may, for example, show a gradual decrease in temperature with depth instead of a sharp thermocline, even if the thermocline is sharp on all individual T-D curves. For that reason, the author developed a technique of averaging the depth of the isotherms. This method, however, cannot be used as widely as the technique of averaging temperatures at various depths; it is mainly applicable to a well-stratified freshwater lake. Both methods are described in the present paper and their relative merits discussed.

A third technique, which is essentially different from these two, has been developed and successfully applied to a large number of ocean data by Pattullo (1952). She analyzed the frequency of occurrence of the thermocline at various levels. The thermocline is, in this case, defined as a layer in which the vertical temperature gradient exceeds an arbitrarily chosen value. A large number

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[1]Received for publication February 21, 1968.
[2]This work was initiated with the Great Lakes Division, Inland Waters Branch of the Department of Energy, Mines and Resources.

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of T-D curves is then scanned for depth-intervals in which the gradient exceeds the chosen value, and the relative frequency of occurrence of these intervals is plotted along the vertical. The "average" depth of the thermocline is indicated by the depth of the interval in which the chosen gradient is exceeded most often. Pattullo's technique can, if necessary, be expanded to include a similar statistical analysis of other structural features of the individual T-D curves.

The first two techniques can be used for any number of data. Pattullo's technique, however, may break down if applied to a small number of observations. Another problem that may arise in the application of the statistical technique is that a critical value has to be assigned to the vertical temperature gradient to define the thermocline before the data can be analyzed.

METHOD

In fresh water with a low content of dissolved or suspended matter, the density of the water is a function of temperature and pressure only. This implies that, when the surface temperature is above the temperature of maximum density, the vertical temperature distribution can be stable only if the temperature is a monotonic decreasing function from surface to bottom. If, on the other hand, the surface temperature is below 4 C, a temperature maximum can occur either at the bottom or at the depth where the T-D curve crosses the line of maximum density (Eklund, 1965).

The T-D curve can, in general, be described as a function $T(z)$ using the temperature T as the dependent variable and the depth z as the independent variable. (Throughout this paper, capitals and corresponding lowercase letters will be used to indicate whether a parameter is considered as a dependent or as an independent variable respectively.) Under certain conditions, however, the T-D curve can also be uniquely defined by $Z(t)$, where the depth Z is given as a function of the independent variable t, the temperature. This holds when the temperature is monotonic increasing or monotonic decreasing from the surface downwards, but not in situations with temperature inversions or with constant temperature over the interval of depth studied.

The function $Z(t)$ can be used to calculate average values for such features of the vertical temperature structure as maximum gradient and depth of thermocline[2] from a number of samples collected either as a time series at a fixed location or at stations distributed evenly over an area of a lake. The only requirement is that the same structural elements appear in all individual samples. This will henceforth be called a homogeneous set of data.

For the purpose of this study, it is assumed that all T-D curves extend well into the hypolimnion, that they show a clear thermocline and a mixed layer near the surface, and that they are monotone decreasing from surface

[2]Depth of thermocline is defined in this paper as the point of maximum gradient as opposed to "Mixed Layer Depth," which is the thickness of the well-mixed layer near the surface and bounded by the surface and a point where the temperature gradient exceeds a certain predefined value for the first time.

to bottom. The observations should form a regular series, taken either at equal intervals of time or in a network of stations distributed evenly over an area. If this is not the case, a correction for irregularities in spacing or timing of the samples can be made by the introduction of weighting factors.

Let us consider a lake of constant depth z_0 on which a large number (I) of T-D curves has been sampled. The observations must form a homogeneous family of curves as described above. An average T-D curve can be defined as a function $\overline{T}(z)$ or as $\overline{Z}(t)$. In general the two curves are different in shape, although the individual $Z_i(t)$ and $T_i(z)$ curves are identical for each value of i. The respective equations are:

$$\overline{T}(z) = \frac{1}{I} \sum_{i=1}^{I} T_i(z) \qquad \ldots\ldots(1)$$

and

$$\overline{Z}(t) = \frac{1}{I} \sum_{i=1}^{I} Z_i(t) \qquad \ldots\ldots(2)$$

where by definition $Z_i(t)$ is taken equal to 0 if $t > t_s$, the surface temperature, and where all T-D curves converge towards the same temperature in the hypolimnion. The definition of $Z_i(t)$ for values of t above the surface temperature implies that no water is present at the station with a temperature $t > t_s$.

The difference between the two average T-D curves is illustrated in Fig. 1 for a set of five hypothetical observations. The fact that $\overline{T}(z)$ is obtained by averaging the data at a certain depth and $\overline{Z}(t)$ by averaging them at a certain temperature is indicated by the horizontal and vertical dotted lines respectively.

Equation 1 gives the relation most widely employed to define an average vertical temperature profile. This definition, however, has its limitations. In the description of an area, the oceanographer or limnologist often distinguishes different water masses by temperature and/or by the concentration of various chemical parameters. The depth z is in this case the dependent variable indicating the level(s) of a characterized water mass. The second definition of an average vertical temperature profile, equation 2, is physically more directly related to the description of observations in terms of water masses, although it cannot be applied as widely as the first method since $Z_i(t)$ may not give a unique definition of the T-D curve for an arbitrarily chosen observation.

The author found that an analysis of data using equation 2, whenever applicable, leads to interesting results that cannot be obtained by the first method. Use of the "average depth" curve $\overline{Z}(t)$, for example, leads to a better description of the temperature profile in the thermocline region. Another interesting property of $\overline{Z}(t)$ is that it is directly proportional to the volume of water with a temperature greater than t, which, in turn, leads to a logical

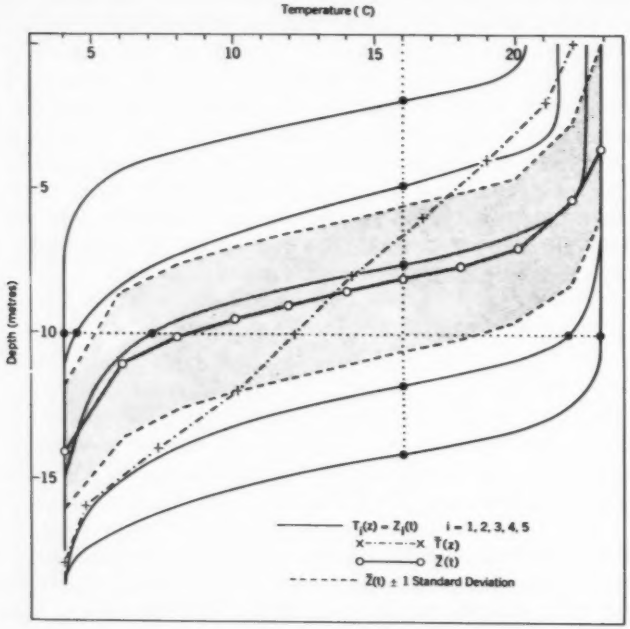

FIG. 1. A hypothetical case of five T-D curves illustrates the computation of, and the differences between, the "mean depth" curve $\overline{Z}(t)$ and the "mean temperature" curve $\overline{T}(z)$. The horizontal and vertical dotted lines indicate the directions along which points of $\overline{T}(z)$ and $\overline{Z}(t)$ are obtained from the individual T-D curves. The heavy black dots mark the intersections between the dotted lines and the individual T-D curves.

manner of defining the epilimnion by a lower limit of temperature. The function $\overline{Z}(t)$ may be especially useful in the study of internal waves since a comparison of the individual data, or of $\overline{T}(z)$, with the "average depth" curve gives an indication of their amplitude.

The relation between tho functions $\overline{T}(z)$ and $\overline{Z}(t)$ and their characteristic properties are examined in the following three sections for the case of a model lake with constant depth z. The statistical significance of the difference between the average curves calculated from an actual set of observations is discussed in a fourth section.

VOLUME AND AVERAGE HEAT CONTENT

The volume of water within a temperature interval (t_1, t_2) is related to the function $\overline{Z}(t)$:

$$\overline{V}\ (t_1, t_2) = \int_{\overline{Z}(t_1)}^{\overline{Z}(t_2)} A\ d\ \overline{Z}\ (t)$$

where A is equal to the area of the lake, which is independent of depth in the present model.

The function $\overline{T}(z)$, on the other hand, can be used to determine the mean heat content of a column of water of unit area extending through an interval of depth (z_1, z_2):

$$\overline{H}(z_1, z_2) = \int_{z_1}^{z_2} \overline{T}(z)\, dz \qquad \ldots\ldots(4).$$

This is equal to the average of the heat contents measured at the individual stations:

$$\overline{H}(z_1, z_2) = \int_{z_1}^{z_2} \overline{T}(z)\, dz = \int \frac{1}{I} \sum_i T_i(z)\, dz = \frac{1}{I} \sum_i \int T_i(z)\, dz$$

$$= \frac{1}{I} \sum_i H_i(z_1, z_2) \qquad \ldots\ldots(5).$$

The total average heat content of a series of observations can be found by integrating equation 4 over the total depth range.

Application of these concepts to the analysis of data sampled on Lake Ontario during the summer of 1966 has given some interesting preliminary results. Definition of the average volume of epilimnion water using $\overline{Z}(t)$ leads to much more consistent results than using $\overline{T}(z)$. The function $Z(t)$ can be used to define a volume average temperature of the epilimnion. Changes in epilimnion temperature can then be correlated with changes in its volume and with external factors. The function $\overline{Z}(t)$ also illustrates clearly that the heat absorbed by the lake during the summer is retained in the gradually thickening epilimnion. Little or no heat is transported into the transition layer or into the hypolimnion.

Vertical Temperature Gradient

For the respective traces $\overline{T}(z)$ and $\overline{Z}(t)$, it can be shown that the gradient of the mean curves for any depth or temperature equals the average of the gradients of the individual curves at the corresponding depth or temperature. The validity of this corollary is limited only in the case of $\overline{Z}(t)$ for temperatures $t > t_{s\,min}$, the minimum surface temperature observed. $\overline{Z}(t)$, however, is still representative of the volume of water within each temperature interval for any temperature observed.

Let $\alpha_i(z)$ be the gradient in degrees C/metre of an individual T-D curve. If t is used as the independent variable, the gradient $\rho_i(t)$ is expressed in metres/degrees C. For an individual curve the following relation holds for each point (t_j, z_j):

$$\alpha_i(z_j) = \frac{1}{\rho_i(t_j)}$$

It can be shown that the average $\bar{\alpha}_i(z)$ of the individual gradients is equal to the gradient $\bar{\alpha}(z)$ of the average temperature function:

$$\bar{\alpha}_i(z) = \frac{1}{I} \sum_{i=1}^{I} \alpha_i(z) = \frac{1}{I} \sum_i \frac{dT_i(z)}{dz} = \frac{d}{dz} \left\{ \frac{1}{I} \sum_i T_i(z) \right\} = \frac{d}{dz} \bar{T}(z).$$

Similarly:

$$\bar{\rho}_i(t) = \frac{d}{dt} \left\{ \bar{Z}(t) \right\}.$$

Contrary to the gradients α_i and ρ_i of the individual observations, the average gradients $\bar{\alpha}(z)$ and $\bar{\rho}(t)$ will not be inverse functions unless $\bar{Z}(t)$ and $\bar{T}(z)$ are identical. This will only occur in the case of a temporal series when the lake has been sampled under a steady state condition or, in the case of a spatial series, when it has been sampled in an area with a uniform temperature at each level.

For an actual set of observations, the maximum gradient of $\bar{Z}(t)$ will usually be much closer to the average of the maximum vertical gradients of the individual observations than the maximum gradient of $\bar{T}(z)$. This is the result of the physical characteristics of the thermocline. Within a homogeneous set of observations, the depth of the thermocline may vary over a large interval, but the temperature at which the maximum gradient occurs is in general much less variable. In most cases it is possible to establish a reference temperature in such a manner that the gradients of all individual T-D curves at this temperature are close to their maximum gradients. This is illustrated by the set of hypothetical observations given in Fig. 1, but it is also true for the Lake Ontario data examined by the author.

Depth of Maximum Gradient

The two traces $\bar{Z}(t)$ and $\bar{T}(z)$ intersect near the point of maximum gradient of $\bar{Z}(t)$, but the latter gives higher temperatures for levels above and lower temperatures for levels below the point of intersection.

This corollary will be proved only for a time series of observations, but similar arguments can be presented for a spatial series. Assume that the depth of the thermocline varies in time only due to movements associated with a single sinusoidal internal wave with an amplitude A and a period P. The T-D curve is a function of time p as well as of depth z and is given by $T(z,p)$ or $Z(t,p)$. For any moment p, $T_i(z)$, and $Z_i(t)$ can be written as the sum of a time-dependent fluctuation and a stationary function $T_0(z)$ or $Z_0(t)$ respectively.

In Fig. 2 the stationary temperature profile (*left*) is perturbed by a sinusoidal internal wave (*right*), and in the lower right hand corner the resultant temperature changes for a depth z_n are shown. Around an arbitrary point (t_n, z_n) the T-D curve can be approximated by two straight lines:

$$T_1(z) = \alpha_1 z \qquad 0 \leq z \leq A$$

for

$$T_2(z) = \alpha_2 z \qquad -A \leq z \leq 0$$

with their origins at (t_n, z_n). The function $T_1(z)$ is constructed in such a manner that the area between the levels z_n and $(z_n$–A), the isotherm t_n, and the function $T_1(z)$ equals the area between z_n, $(z_n$–A), t_n, and $T_0(z)$. The function $T_2(z)$ can be constructed analogously. This is only a crude approximation of the T-D curve, but it serves to illustrate the present point.

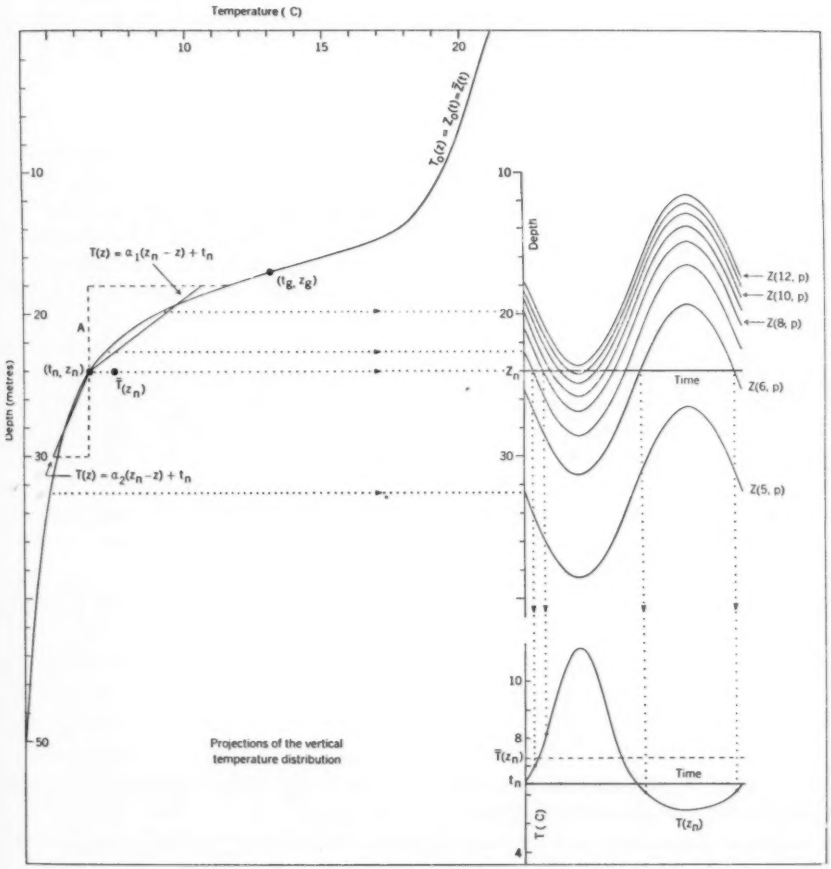

FIG. 2. A stationary temperature profile (*left*) is perturbed by a sinusoidal internal wave (*right*). Projections of the perturbed temperature structure in the time–depth plane and in the time–temperature plane are indicated on the right. The latter projection gives changes in temperature at the depth z_n. The change in the average temperature measured at the depth z_n is given by $\bar{T}(z_n)$–t_n.

The changes in time of the temperature at the depth z_n are expressed by:

$$T(z_n, p) = t_n + \alpha_1 A \sin (2\pi \frac{p}{P}) \quad \text{for} \quad 0 \leq p \leq \frac{P}{2}$$

$$T(z_n, p) = t_n + \alpha_2 A \sin (2\pi \frac{p}{P}) \quad \text{for} \quad \frac{P}{2} \leq p \leq P.$$

The average temperature at the depth z_n over one full period of the wave can now be calculated:

$$\begin{aligned} \overline{T}(z_n) &= \frac{1}{P} \int_0^P T(z_n, p) dp \\ &= \frac{1}{P} \left\{ \int_0^{\frac{P}{2}} \alpha_1 A \sin (2\pi \frac{p}{P}) dp + \int_{\frac{P}{2}}^P \alpha_2 A \sin (2\pi \frac{p}{P}) dp \right\} + t_n \\ &= \frac{A}{\pi} (\alpha_1 - \alpha_2) + t_n \qquad \ldots\ldots(8). \end{aligned}$$

It is seen that $\{\overline{T}(z_n) - t_n\}$ is a function of depth, since α_1 and α_2 depend on the choice of (t_n, z_n), and that the difference will be positive or negative depending on whether $\alpha_1 > \alpha_2$ or $\alpha_1 < \alpha_2$ for that depth. It is also obvious that the two temperatures $\overline{T}(z_n)$ and t_n are identical only if $\alpha_1 = \alpha_2$, which, for a finite amplitude of the internal wave, will be near the point of maximum gradient. For an infinitely small amplitude, or if the T-D curve is symmetrical around the point of maximum gradient, the two curves will intersect at the point of maximum gradient of $\overline{Z}(t)$.

The average depth of the isotherm t_n, on the other hand, does not depend on the gradient of the T-D curve around (t_n, z_n) and is given by:

$$\overline{Z}(t_n) = \int_0^P A \sin (2\pi \frac{p}{P}) dp + Z_0(t_n) = Z_0(t_n) \qquad \ldots\ldots(9).$$

The average curve $\overline{Z}(t)$ is thus identical to $Z_0(t)$, since equation 9 holds regardless of the choice of (t_n, z_n).

Similar arguments can be used to prove the corollary in the general case when the only restriction on the observations is that they form a homogeneous family of curves. $\overline{Z}(t)$ and $\overline{T}(z)$ will still intersect near the point of maximum gradient of $\overline{Z}(t)$, the latter will still show higher temperatures than $\overline{T}(z)$ above the level of maximum gradient and lower temperatures below it, and the difference between the two temperatures at any level is still given by equation 8. The gradients α_1 and α_2 are now the average gradients of the computed

function $\overline{Z}(t)$ above and below the arbitrary point (z_n, t_n). The quantity A is, for a given mean temperature profile $\overline{Z}(t)$, a measure of the observed vertical variability of the data. It can be interpreted in terms of an average wave height if the fluctuations between the observations are of a random nature, that is, if they are not caused by a trend in the case of a temporal series or by a time-independent horizontal gradient in the case of a spatial series.

In the example presented in Fig. 2 an internal wave with an amplitude of 6 m is shown. The average temperature measured at a depth $z_n = 24$ m over one full period of the wave can be calculated from equation 8:

$$\overline{T}(24) = t_n + \frac{6}{\pi}(0.69\text{–}0.22) = t_n + 0.9 \qquad \ldots\ldots(10).$$

As a result of vertical movements of the thermocline caused by the internal wave, the average temperature measured at this particular depth is increased by 0.9 C as compared with the temperature that would have been measured in a stationary distribution! This computed change in temperature is somewhat lower than the actual change due to the nature of the approximation of the T-D curve around the depth z_n.

Confidence Limits of $\overline{Z}(t)$ and $\overline{T}(z)$

Confidence limits of points of the calculated "average depth" curve $\overline{Z}(t)$ can be found if it is assumed that the distribution of $Z_i(t)$ is normal for any given temperature t:

$$-k\frac{\sigma(t_n)}{\sqrt{N}} < \overline{Z}(t_n) - \overline{Z}_0(t_n) < k\frac{\sigma(t_n)}{\sqrt{N}} \qquad \ldots\ldots(11)$$

(Mandel, 1964), where k is a factor determined by the required probability interval and $\sigma(t_n)$ the standard deviation of $Z_i(t_n)$ for given t_n. For $N \gg 10$ the 90% and 95% confidence limits correspond to $k = 1.64$ and $k = 1.96$ respectively. The distribution of $Z_i(t)$ has been tested for a large number of summer observations collected in Lake Ontario; in the thermocline region it is sufficiently close to normal for equation 11 to give reasonable results.

A similar relation can be given for the confidence limits of the mean temperature curve. The distribution of $T_i(t)$, however, has a much larger tendency towards being skewed or even bimodal than $Z_i(t)$, thus severely limiting the applicability of the equation.

RESULTS

The different properties of the functions $\overline{T}(z)$ and $\overline{Z}(t)$ are illustrated in Fig. 3, which is based on a set of observations taken at a series of regularly spaced stations in the central part of Lake Ontario in late August 1966. A comparison of the two curves shows that they intersect near the point of maximum gradient of $\overline{Z}(t)$ and that the maximum gradient of the latter, 1.4

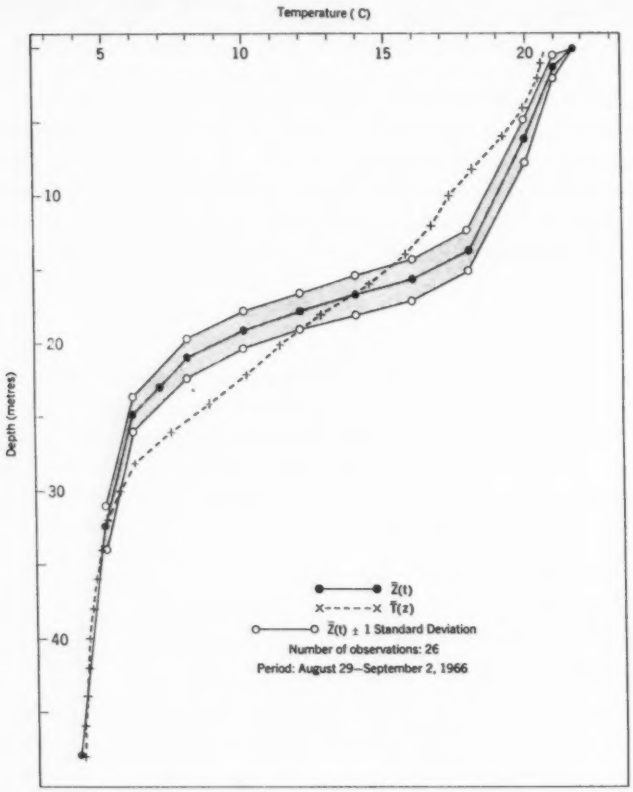

FIG. 3. $\bar{Z}(t)$ and $\bar{T}(z)$ from a set of experimental data on Lake Ontario.

degrees C/metre, is much higher than the maximum gradient of $\bar{T}(z)$, which is 0.7 degrees C/metre. The average of the maximum gradients of the individual curves is 1.5 degrees C/metre.

The difference in the gradients of $\bar{Z}(t)$ and $\bar{T}(z)$ is a direct result of the structure of the thermocline. Throughout the summer of 1966, the maximum gradient of almost all individual BT's sampled on any cruise occurred within a fixed 6 C interval. The gradient usually did not vary much within this interval. The depth of the thermocline, on the other hand, fluctuated over an interval of 20 m, excluding near-shore upwelling areas. Within this interval the gradient of each individual BT varied from close to zero to its maximum value. The reason for this is obvious since the average maximum gradient is 1.5 degrees C/metre, whereas the total temperature difference between surface and bottom is only in the order of 16–20 degrees C. The gradients of the individual observations at a specific depth thus range over a much wider

interval than those at a specific temperature, which is reflected in the differenec between the maximum gradients of $\bar{Z}(t)$ and $\bar{T}(z)$.

In Fig. 3 the 68% confidence limits (1 standard deviation) for $\bar{Z}(t)$ are indicated, showing that the difference between the two mean curves $\bar{Z}(t)$ and $\bar{T}(z)$ is highly significant. This difference is caused by a combination of two factors. A study of the horizontal distribution of the depth of the thermocline shows a distinct relation between observed depth and location, and superimposed on this is a random variation that can be attributed to internal waves. The wave height of these internal waves can be estimated using equation 8, provided that the data can be adjusted for the nonrandom local variations in the depth of the thermocline. To illustrate this point, let us assume that the data have been adjusted and that at a point $(t_n, z_n) = (8, 20)$ on $\bar{Z}(t)$ the following quantities are measured: $\bar{T}(20) = 8.8$ C, $\alpha_1 = 1.3$ degrees C/metre, and $\alpha_2 = 0.6$ degree C/metre. The estimated wave height would then be

$$A = \frac{8.8-8.0}{1.3-0.6} \times \pi = 3.6 \text{ (m)}.$$

The Lake Ontario data analyzed so far did not show any temperature inversions during the summer. Occasionally, however, the temperature remained constant over a certain interval of depth. This was, for example, sometimes found when the epilimnion was particularly well mixed. If the region with a constant temperature occurred respectively above or below the depth of maximum gradient, the lowest or highest levels at which that particular temperature was observed were chosen to define $Z_i(t)$. This does not affect the results to any appreciable extent if the intervals at which $Z_i(t)$ have been read are sufficiently small.

CONCLUSIONS

In the case of a stratified freshwater body, the characteristics of the thermocline, such as depth and maximum gradient, can be described more realistically by $\bar{Z}(t)$ than $\bar{T}(z)$, especially if the depth of the thermocline varies widely between samples.

One of the main advantages of averaging the depth of the isotherms instead of the temperature at each level is that the vertical temperature profile of the resulting mean curve $\bar{Z}(t)$ is much more closely related to the individual T-D curves than $\bar{T}(z)$, especially in the thermocline region. It has been shown that the maximum gradient of $\bar{Z}(t)$ is about equal to the average of the maximum gradients of the individual curves, whereas the maximum gradient of $\bar{T}(z)$ could be much smaller. Differences between the two curves can give an indication about the height of internal waves. $\bar{Z}(t)$ is proportional to the volume of water warmer than t C; the integral of $\bar{T}(z)$, on the other hand, is a measure of the heat content of the lake down to a certain depth.

Application of this "average-depth-of-isotherm" method on a large number of observations collected on Lake Ontario in the summer of 1966

has proved to be fruitful. Instabilities in the temperature profiles, which would cause a nonunique definition of individual T-D curves by $Z_i(t)$, did not occur or were so small in magnitude that they did not appreciably influence the calculations.

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A Review and Description of *Caligus curtus* Müller, 1785 (Caligidae: Copepoda), Type Species of its Genus[1]

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ABSTRACT

The synonomy, known distribution, and hosts of *Caligus curtus* Müller, 1785 are reviewed. As a basis for comparison with its congeners, a description with illustrations is given. Homology of the thoracopods and functional morphology of the mouth cone and sternal furca are discussed.

INTRODUCTION AND HISTORICAL REVIEW

In the 183 years since O. F. Müller (1785) introduced the name *Caligus curtus* for a common caligid parasite of *Gadus merlangus* (now *Merlangus merlangus*) in Danish waters, this copepod has been mentioned, reported, or discussed in no less than 150 different publications. Prior to Müller's naming of this species, it was included in the all-embracing *Monoculus piscinus* Linnaeus (also known as *Binoculus piscinus* and later as *Caligus piscinus*). Even Müller himself accepted more than one species under the name *C. curtus*, as evidenced by his consideration (p. 132) that previously reported specimens from several fishes, including salmon, from the North Atlantic and adjacent waters belonged to this species. The salmon is not a host of *C. curtus* but carries its own caligid, *Lepeophtheirus salmonis* (Krøyer, 1837).

For precisely how many years zoologists have been aware of this species is unknown but certainly the period spans more than two centuries. Like so many other animals with a similarly long history, *C. curtus* has accumulated a number of synonyms (see Krøyer, 1837; Steenstrup and Lütken, 1861; Olsson, 1869; Bassett-Smith, 1899; Wilson, 1905; Brian, 1906; Scott and Scott, 1913; Dollfus, 1953; Markevich, 1956; Yamaguti, 1963). In part, some of the synonymy resulted from the failure of early 19th century workers to recognize sexual differences within the species, i.e., males and females were considered as distinct species.

The accepted synonyms of *C. curtus* include *C. mülleri* Leach, 1816; *C. bicuspidatus* Nordmann, 1832; *C. americanus* Pickering and Dana, 1838; *C. diaphanus* of Baird, 1850; *C. elegans* Van Beneden, 1851; *C. fallax* Krøyer, 1863; and *C. aeglefini* Krøyer, 1863. At least three other species (*C. rissonianus* Milne-Edwards, 1840 (*lapsus* for *rissoanus*); *C. lacustris* Steenstrup and Lütken,

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1861; and *C. bifurcus* Shen, 1958) have been proposed as synonyms (Wilson, 1905, p. 555; Brian, 1906; Yamaguti, 1963) of *C. curtus* but these have not generally been accepted.

Caligus curtus is essentially a parasite of the external surfaces of marine gadids, particularly *Gadus morhua*, but it has been reported from a variety of other marine fishes, including elasmobranchs (Table I). The report by Baird (1850) of its occurrence in the freshwater fish *Coregonus pollan* in Lough Neagh (Northern Ireland) is, indeed, suspect; the validity of this identification was first questioned by Scourfield (1903). It is not unlikely that some of the records included in Table I may be based on misidentifications but in the absence of accompanying descriptions or figures, critical judgement is not possible. Although *C. diaphanus* of Baird, 1850, is now commonly accepted as a synonym of *C. curtus*, we have intentionally omitted from this table Baird's list of hosts of his *C. diaphanus* because there is no way of knowing if the specimens from all the reported hosts were identical with *C. curtus*. In this regard we draw special attention to Wilson's (1908, 1936) records from *Mugil cephalus* at Beaufort, North Carolina, and from plankton at Bermuda, because they are outside the established range for *C. curtus*. We have been unable to locate Wilson's specimens, and consequently these records could not be verified.

The Arctic-Boreal region of the Atlantic Ocean and contiguous waters (Fig. 1, Table I) includes the natural range of this species. Several reports of the species occurring outside this region cannot be accepted at face value. For example, Tilesius (1815) claimed to have taken varieties of *C. curtus* from salmon in the Pacific waters off Kamchatka, USSR, and from *Coryphaena hippurus* and *Squalus* sp. from the Brazilian coast. The species taken from salmon must have been *Lepeophtheirus salmonis* (Krøyer, 1837), the common and only caligid occurring on both Pacific and Atlantic salmons (Margolis, 1958). The identity of the Brazilian material will never be known with certainty but it is worth noting that the more recent records of *Caligus* species from *Coryphaena* species do not include *C. curtus*. Kirtisinghe (1964) reported this species from *Pristipomoides typus* from Ceylon but it is clear from his figures that the identification is an error. The general shape and body proportions are sufficiently different from *C. curtus* to exclude these Indian Ocean specimens from this species. Heegaard (1945) included the Indian Ocean in the distributional range of *C. curtus*, but the source of this information eludes the present authors.

The reports by Brian (1898, 1906) of the occurrence of *C. curtus* on *Lichia amia* and *Mugil cephalus* from Mediterranean waters in the vicinity of Italy were subsequently corrected by him. His material from *L. amia* was described (Brian, 1906) as a new species, *C. lichiae*, and the material from *M. cephalus* eventually formed the basis of his (Brian, 1935) new variety *C. minimus* var. *mugilis*. Evidently, no valid records of *C. curtus* from the Mediterranean region exist in Brian's publications. Heegaard (1943) reported this species from the Adriatic Sea (the host was not stated) on the basis of material pre-

served in the Riksmuseum, Stockholm; neither description nor figures were presented. Through the courtesy of Dr Roy Oleröd of the Riksmuseum, Stockholm, the material (one female) identified by Heegaard was made available to us, and its specific identity was confirmed. However, from the accompanying labels we could not corroborate that the specimen came from the Adriatic Sea, and Dr Oleröd's investigation of the Museum's records showed that the specimen was obtained from Hamburg in 1869 and that its alleged Adriatic origin is unsupported. A number of authors (e.g., Wilson, 1932; Pesta, 1934; Polyansky, 1955; Markevich, 1956; Yamaguti, 1963) have included the Mediterranean as part of the range of *C. curtus*. However, there is no evidence to support the occurrence of *C. curtus* in this sea.

The basis for Markevich's (1956) inclusion of the Baltic Sea in his summary of the distribution of *C. curtus* is unknown to us. We are unaware of any other reports of this species from the Baltic, and it is not clear if Markevich's citation is based on previously unpublished information.

Yamaguti's (1963) relegation of *C. bifurcus* Shen, 1958, to the synonymy of *C. curtus*, thereby extending the range of *C. curtus* into Pacific waters, cannot be accepted. From Shen's (1958) description and figures it is clear that there are a number of differences (e.g., the armature of the 1st and 4th thoracopods) between *C. bifurcus* and *C. curtus*.

Although a number of descriptions of *C. curtus* have been published (Müller, 1785; Johnston, 1824, as *C. mülleri*; Krøyer, 1837; Pickering and Dana, 1838, as *C. americanus*; Nordmann, 1832, as *C. bicuspidatus*; Van Beneden, 1851, as *C. elegans*; Wilson, 1905; Scott and Scott, 1913; Dollfus, 1953; Markevich, 1956) and the species apparently is readily recognized among copepod collections from North Atlantic fishes, there are many structural details which remain undescribed. Since *C. curtus* is the type species of its genus, it seemed to us highly desirable to present a detailed description of it which could be used as a basis for comparison with other species of *Caligus*.

MATERIALS AND METHODS

The major material examined was a collection containing about 200 *C. curtus*, obtained by the second author from cod (*Gadus morhua*) in Scottish waters. In addition, a large collection from various hosts was made available for study by the Zoological Museum, University of Copenhagen. Grosser details were observed with a binocular dissecting microscope, with magnifications up to 100 diam. Finer structures were examined with a compound microscope, usually at 400 magnifications or less. Occasionally we resorted to the use of Nomarsky Interference Phase at up to 940 magnifications. Serially mounted longitudinal and cross sections, cut at 10 μ thickness, were prepared and stained with haematoxylin–eosin. Whole animals were studied in alcohol without stain, and in lactic acid both with and without staining with fast green. Dissected parts were usually mounted in polyvinyl alcohol. Drawings were usually made with a camera lucida; however, in some cases an eyepiece graticule with an engraved grid was used.

TABLE I. Host and locality records of *Caligus curtus*.[a]

Hosts[b]	Localities	Authors[c]
Chondrichthyes — cartilaginous fishes		
Squaliformes		
Squalidae		
Squalus acanthias syn. *Acanthius vulgaris*	Skagerrak-Kattegat (Scandinavia)	Olsson, 1869
Rajiformes		
Rajidae		
Raja batis	Skagerrak-Kattegat	Olsson, 1869
	Scotland	Scott, 1900
Raja fullonica	Skagerrak-Kattegat	Olsson, 1869
Raja laevis	Atlantic coast (Maine to New York), USA	Rathbun, 1885; Wilson, 1905
Raja maculata	Belfast Bay, Northern Ireland	Thompson, 1847
Raja oxyrhynchus	Scotland	Scott, 1900
Raja radiata	Skagerrak-Kattegat	Olsson, 1869
Chimaeriformes		
Chimaeridae		
Chimaera monstrosa	Skagerrak-Kattegat	Olsson, 1869, 1896
Osteichthyes — bony fishes		
Gadiformes		
Gadidae		
Brosme brosme syn. *Brosmius brosme*	Scotland	Scott, 1900
Gadus minutus	Plymouth, England	Leigh-Sharpe, 1926
Gadus morhua syns. *G. callarias*, *Morrhua vulgaris*	British Isles (including North Sea coast, English Channel, and Irish Sea)	Leach, 1816[d]; Johnston, 1824[d] Baird, 1850[d]; Miers, 1880; Thompson, 1893; Bassett-Smith, 1896; Scott, 1904; Leigh-Sharpe, 1926
	Scandinavian waters (North Sea, Skagerrak-Kattegat) to Belgium	Krøyer, 1837; Van Beneden, 1851[e]; Olsson, 1869; Timm, 1894; Heegaard, 1947

	Barents Sea	Bazikalova, 1932; Markevich, 1936; Polyansky, 1955; Polyansky and Kulemina, 1963
	Faroe Islands	Hansen, 1923; Stephensen, 1929
	Iceland	Hansen, 1923; Leigh-Sharpe and Perkins, 1924; Stephensen, 1940
	Greenland	Stephensen, 1913; Wilson, 1920; Hansen, 1923
	Atlantic coast of Canada to New York, USA	Pickering and Dana, 1838[f]; Verrill, 1873; Rathbun, 1885; Wilson, 1905; Stock, 1915; Bere, 1930; Heller, 1949
Melanogrammus aeglefinus syns. *Gadus aeglefinus*, *Aeglefinus melanogrammus*	Belfast Bay, Northern Ireland	Baird, 1850
	Danish waters	Krøyer, 1837
	Barents Sea	Bazikalova, 1932; Markevich, 1936; Polyansky, 1955
	Faroe Islands	Hansen, 1923
	Iceland	Hansen, 1923; Stephensen, 1940
	Greenland	Wilson, 1920
	Atlantic coast of Canada to New York, USA	Wilson, 1905; Brian, 1914; Stock, 1915; Bere, 1930
Merlangus merlangus syns. *Gadus merlangus*, *Merlangus vulgaris*	Danish waters; eastern Skagerrak	Müller, 1785; Heegaard, 1947
	Belfast Bay, Northern Ireland	Baird, 1850[d]
Merluccius bilinearis	Atlantic coast of Canada	Stock, 1915
Merluccius merluccius syn. *M. vulgaris*	Scotland; Irish Sea	Scott, 1900; Scott, 1904
Microgadus tomcod	Atlantic coast of Canada	Stock, 1915; Bere, 1930
Molva byrkelange	Faroes; Iceland	Hansen, 1923; Stephensen, 1929
Molva molva syns. *M. vulgaris*, *Gadus molva*	Scotland; Irish Sea	Scott, 1900; Scott, 1904
	North Sea coast of Norway	Rathke, 1843
	Skagerrak-Kattegat	Olsson, 1869
	Iceland	Stephensen, 1940

(*Continued*)

TABLE I. Host and locality records of *Caligus curtus*.[a] — (*Concluded*)

Hosts[b]	Localities	Authors[c]
Pollachius pollachius	Baie de Concarneau, France	Guiart, 1913
syns. *Gadus pollachius*,	Eastern Skagerrak	Heegaard, 1947
Merlangus pollachius	Belfast Bay, Northern Ireland	Baird, 1850[d]
Pollachius virens syn. *Gadus virens*	Skagerrak-Kattegat	Olsson, 1869; Heegaard, 1947
	Barents Sea	Polyansky, 1955
	Iceland	Leigh-Sharpe and Perkins, 1924; Stephensen, 1940
	Atlantic coast of Canada and USA	Wilson, 1905; Stock, 1915; Bere, 1930
Urophycis tenuis syn. *Phycis tenuis*	Atlantic coast of USA	Rathbun, 1885; Wilson, 1905
Perciformes		
Scorpaenidae		
Sebastes norvegicus	Skagerrak-Kattegat	Olsson, 1869
Triglidae		
Trigla gurnardus	Skagerrak-Kattegat	Olsson, 1869
Mugilidae		
Mugil cephalus	Beaufort, North Carolina, USA	Wilson, 1908
Mugil chelo	Belfast, Northern Ireland	Baird, 1850[d]
Pleuronectiformes		
Bothidae		
Scophthalmus laevis	Belfast Bay, Northern Ireland	Baird, 1850[d]
Scophthalmus maximus	Belfast Bay, Northern Ireland	Baird, 1850[d]
syns. *Rhombus maximus*, *R. vulgaris*	Belgium (Ostende)	Schuurmans-Stekhoven, 1936
	Southwest Sweden (eastern Skagerrak)	Heegaard, 1945
Pleuronectidae		
Hippoglossus hippoglossus	Atlantic coast of USA	Wilson, 1905
syn. *H. vulgaris*	Faroes; Iceland	Hansen, 1923; Stephensen, 1940

	Locality not specified (presumably Barents Sea)	Markevich, 1956
Pleuronectes platessa	British Isles	Baird, 1850[d]; I.C. Thompson, 1893; T. Scott, 1900; A. Scott, 1904
Lophiiformes		
Lophiidae		
Lophius piscatorius	Skagerrak-Kattegat	Olsson, 1869
In plankton	Bermuda	Wilson, 1936

[a]Excluded from this table are reports of *C. curtus* which have subsequently been shown to be misidentifications or which we believe to be misidentifications.

[b]Host nomenclature and classification generally follow American Fisheries Society (1960). Synonyms listed are only those used by authors in reporting *C. curtus*, under this name or one of its synonyms.

[c]The cited authors are restricted almost entirely to those responsible for the actual records.

[d]Reported as *C. mülleri*.

[e]Reported as *C. elegans*. Van Beneden's (1861, 1871) citations of *C. curtus* from "*Gadus callarias, Gadus aeglefinus, Morrhua vulgaris, Morrhua aeglefinus*, and *Lota molva*" are not included here as they seem to be based on reports by previous workers. However, many recent authors consider them to be original records from the coast of Belgium.

[f]Reported as *C. americanus*.

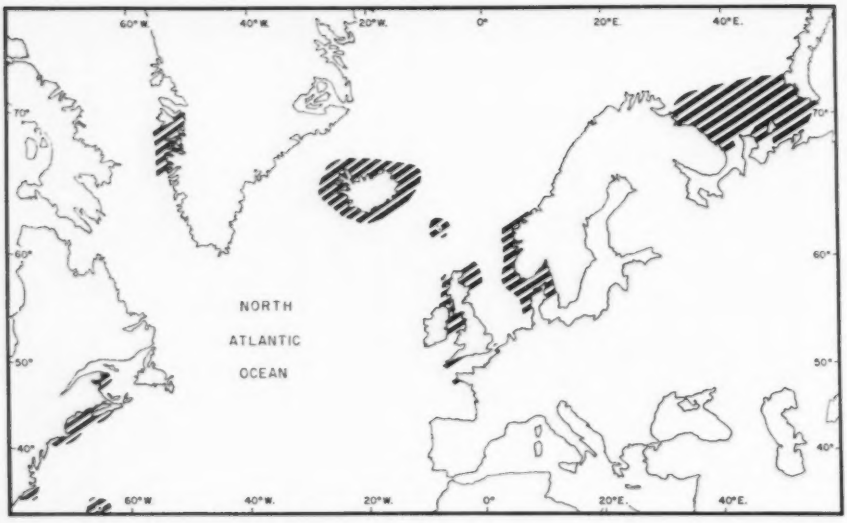

FIG. 1. Known distribution of *Caligus curtus* Müller, 1785.

DESCRIPTION

GENERAL APPEARANCE

Seen from the dorsal aspect (Fig. 2) the female of *Caligus curtus* clearly shows two main regions: anteriorly, the cephalothorax and, posteriorly, the 4th and genital thoracic segments and the abdomen. In ovigerous specimens, a pair of tubular egg strings are seen trailing posteriorly from the genital segment. The male (Fig. 6) is distinguishable from the female by the relatively smaller size and form of the genital segment and by the relatively greater width of the cephalothorax.

The carapace, shaped like a shield with a rounded anterior, covers the anterior appendages. The part covered by the carapace consists of several thoracic segments fused with the cephalon and constitutes, therefore, a true cephalothorax. When in position on its host fish, *Caligus* adheres tightly to the integument with its anterior part, facing the direction of the host's movement. The narrower posterior part is raised above the surface of the host, being trailed behind the cephalothorax in the water current generated by the forward motion of the host.

The carapace is divided by suture lines into four areas (Fig. 2, 6). These were named by Wilson (1905) the cephalic area (*ca*), the thoracic area (*ta*), and the two lateral areas (*la*). These terms are used here, but it must be emphasized that the cephalic and thoracic areas of the carapace do not correspond to the cephalic and thoracic regions of the cephalothorax. The thoracic area extends caudally between the posterior halves of the lateral areas and ends as the posterior margin of the carapace. This margin is indented on either side to form two sinuses (*ps*, Fig. 2, 6).

The anterior region of the cephalothorax is formed by the frontal plates (*fp*, Fig. 2–7). At the midanterior line a notch partially separates these plates. This area contains the median cement gland which secretes the frontal filament of the chalimus stages. Both plates have, near the middle of their anterior margins, a small, naked seta. The entire length of these margins is rimmed with a finely striated, hyaline membrane, similar to those found on other parts of the cephalothorax. Laterally, where the rounded ends of the frontal plates join with the cephalic area, deep notches are formed, partially enclosing the bases of the 1st antennae. On the ventral

surface of each frontal plate, somewhat laterally, a lunule is found (*l*, Fig. 2–4, 6, 7) and its position is detected in dorsal aspect by a relatively thin semicircular area on the margin of the frontal plate. Both the antennae and the lunules will be described in detail later.

From the bases of the 1st antennae two pairs of oblique grooves run inwards over the surface of the cephalic area. The medial pair of these grooves is the longer and more prominent, extending quite close to the median paired eye. The median eye (*e*, Fig. 2, 6), of the usual caligid structure, is situated just anterior to the centre of the cephalic area.

The lateral margins of the carapace are formed anteriorly by the cephalic and posteriorly by the lateral areas. They diverge slightly to give the carapace its greatest width about midway between the transverse suture and the posterior margin. Anteriorly the lateral margins are not quite smooth. Irregular notching occurs near the bases of the 1st antennae. Shallow indentations are usually associated with the end points of the longitudinal sutures. In dorsal aspect one can also see, more or less clearly, a notch at about the midlength of the carapace (*mn*, Fig. 2, 6). This notch is associated with the end of a ridge running over the ventral surface of the cephalothorax. The posterior halves of the lateral margins are smooth and curve in to meet the posterior sinuses and to form the major part of the rounded lobes. Both margins are provided along their entire length with a finely striated, marginal membrane (*mm*, Fig. 2–7). This membrane is about four times as wide as that fringing the margins of the frontal plates. Figures 22 and 23 make clear the nature of this membrane, which is a cuticular extension produced at the point of meeting of the dorsal and the ventral surfaces of the cephalothorax. The only remaining marginal membranes of the carapace are a pair attached to the fingerlike extensions of the thoracic area forming the lateral boundaries of the posterior sinuses. At the level of the anterior end of the posterior sinuses, each lateral area has, on its dorsal surface, a pitlike depression. These depressions (*sc*, Fig. 2, 3, 5, 6), because of their particularly good supply of minute branched setules, which are shown later to be sensory in nature, are referred to here as "sensory crypts." Their specific function is unknown.

The posterior margin of the cephalothorax articulates with the 4th thoracic segment. In contracted specimens it partially overlies this segment (Fig. 5). The 4th thoracic segment is short and broad, and laterally equipped with the 4th pair of thoracopods, partly exposed in the dorsal aspect. The spaces lateral and anterolateral to the 4th segment are filled with the lamelliform 3rd thoracopods, which extend between the posterolateral tips of the carapace and the anterolateral corners of the genital segment.

The remainder of the thorax forms the genital segment. Wilson (1905) considers it to consist of a single segment, although the presence of two pairs of vestigial thoracopods on this segment in many species of *Caligus* males suggests that two segments have been incorporated in its structure (Heegaard, 1947). It is in the shape of the genital segment that differences between the two sexes of *C. curtus* are most obvious.

The genital segment of the mature female (*gs*, Fig. 2–4) is longer than wide, its width being about half that of the carapace. The anterior end of the segment is broadly rounded. Its lateral margins are roughly parallel to each other. The central part of the posterior margin forms the junction between the genital segment and the abdomen. The posterior margin runs transversely to the long axis of the body and on its posterolateral corners are the 5th thoracopods, represented by two papillae bearing setae (*th* 5, Fig. 2, 4). Observed from the ventral aspect, the genital segment shows the openings of the oviducts, which are situated anterolaterally to the junction between the genital segment and the abdomen. The posterolateral corner of the genital segment is shown in detail in Fig. 12. Just medial to the orifice of the oviduct is a short, rather irregular outgrowth, the medial process (*mp*, Fig. 12).

The genital segment of the male (*gs*, Fig. 5–7) is proportionately smaller and more rounded in outline, with the exception of the posterolateral corners, shown in detail in Fig. 11. Seen in ventral aspect, this corner displays clearly two processes, medial and lateral (*mp*, *lp*, Fig. 11). The lateral process carries the 5th thoracopod, and the flat, broad medial process represents the site of the 6th thoracopod.

The abdomen of the female (*abd*, Fig. 2–4) is 1-segmented, roughly quadrangular, slightly narrowed anteriorly and posteriorly. The posterior margin forms an obtuse angle bisected by

the anal opening. Associated with each side is a caudal lamella. These lamellae are flattened and roughly quadrangular.

The abdomen of the male (*abd*, Fig. 5–7) is proportionately larger, also 1-segmented. Its anterior end forms a less accentuated "waist" than that of the female, its caudal lamellae are rather longer but otherwise similar to those of the female.

The dorsal surface of the cephalothorax and, to a lesser extent, also the other parts of the body, are equipped with scattered minute setules. These setules are generally of two types as shown in Fig. 10. One type is simple (Fig. 10*b*) with a broad base and very fine tip, whereas the other type (Fig. 10*a*) is irregularly branched, and arises from a base similar to the first type.

The setules of both types are distributed in different ways over the surface of the body. The complex setules (Fig. 10*a*) are arranged in a constant pattern, shown in Fig. 8 and 9 by circles. The pattern is bilaterally symmetrical and appears to be quite constant in all the specimens examined. These setules are most common on the cephalic area of the carapace, although they occur also on the lateral areas (particularly in association with the sensory crypts), as well as on the thoracic area. They are also present on the free thoracic segment and a few of them are found on the genital segment. On the abdomen there are only two (Fig. 9), at some distance from the caudal lamellae. The simple setules (dots in Fig. 8 and 9) are much more numerous and far less constant in distribution. They do not form strict bilateral patterns. A row of closely spaced setules of this simple type is found along the margins of the lateral areas. At the point of the greatest width, this row is interrupted by the presence of a similar setule, which, however, is much longer than the others (Fig. 2, 4, 6, 7). It is on the lateral areas of the carapace that the simple setules are most abundant (Fig. 8). Several of them are also scattered over the cephalic and thoracic area, one occurring even on each frontal plate. The surface of the genital segment does not show many but they are quite common on the dorsal surface of the abdomen and on the caudal lamellae (Fig. 9).

The ventral surface of the cephalothorax is divisible into several regions. The posterior limit of the cephalic region is marked ventrally by ridges (*pcr*, Fig. 4, 7) which arise at the bases of the maxillae[2] and run in a posterolateral direction. It is at the end of these ridges that one observes from the dorsal aspect, as previously mentioned, the notch in the lateral margin of the carapace. The relatively flat area in front of these ridges provides the surface of attachment for the cephalic appendages. The most anterior of these are the 1st antennae (*ant* 1, Fig. 2–4, 6, 7). Posteromedial to the 1st antennae are the 2nd antennae (*ant* 2, Fig. 4, 7). The ventral surface of the cephalothorax, directly lateral to the bases of the 2nd antennae, is hollowed out, forming a groove (*g*, Fig. 30–32) into which the appendages can be partially withdrawn. Posterolateral to the 2nd antennae are the postantennal processes (*pap*, Fig. 4, 7). The medial mouth cone (*mc*, Fig. 4, 7) is flanked by the postoral processes (*pop*, Fig. 4, 7). Level with the ventrally projecting tips of these processes are the bases of the maxillae (*mx*, Fig. 4, 7) and the medial limits of the posterocephalic ridge. Oblique, wide grooves run immediately behind these ridges and accommodate the basal parts of the maxillae, when retracted. Between the ridges and the posterior limit of the cephalothorax, the ventral surface of the cephalothorax is divided into three longitudinally disposed regions. The flat central region is raised above the level of the two lateral regions which appear as two cavities. These lateral cavities are traversed by a pair of internal cuticular ribs (*por*, Fig. 4, 7), which run obliquely backwards and gradually diminish in size, until they disappear near the lateral margins of the cephalothorax. It is this pair of ribs that is frequently shown in the dorsal view of *Caligus*, since it is visible through the thickness of the carapace. The anterolateral portions of the central flat area provide attachment for the maxillipeds (*mxp*, Fig. 4, 7), while its centre is occupied by the sternal furca (*sf*, Fig. 4, 7). Behind the sternal furca it is traversed by the interpodal bars, structures linking the right and left thoracopods. The 3rd interpodal bar forms the central part of the apron developed from it and the 3rd pair of

[2]A controversy over the analogy and correct naming of the maxilla and maxillipeds presently exists (Lang, 1948; Heegaard, 1947, 1948; Ferris and Henry, 1949; Lewis, 1963, 1964). The present authors, in designating names to these appendages, do not wish to imply that they have solved this controversy. Names used are simply an expediency until the matter can be settled.

thoracopods (*th* 3, Fig. 4, 7). The apron completes the posterior boundary of the concavity formed by the ventral surface of the cephalothorax.

Directly behind the 1st interpodal bar, the ventral surface of the body carries two small, semispherical swellings, tipped with short, simple setules (*s*, Fig. 4, 7). The nature of these structures is not as yet understood.

The Frontal Plates (Fig. 13–21, 29)

The lateral extremity of each frontal plate (Fig. 13, 14) forms a rounded extension which lies partly over the dorsal surface of the 1st antenna. Directly proximal to the base of the 1st antenna, the plate is joined with the anterior margin of the carapace by a rather complicated articulation surface (*a*, Fig. 14). On the anterior margin of the frontal plate there is an auxiliary organ of attachment known as a lunule. The structure of the lunule is illustrated by sections (Fig. 17, 18) passing through planes indicated in Fig. 15. As mentioned earlier, the margin of the frontal plate is provided with a narrow membrane (*m*, Fig. 16). It appears that this membrane has become modified into the lunule, involving also a part of the plate itself. The membrane widens gradually (Fig. 17) into an almost circular structure (*l*, Fig. 13–15), which is covered dorsally by the frontal plate. A part of the lunule is exposed (Fig. 13) by a curved indentation in the margin of the plate at that region (*ind*, Fig. 17). The sections show that these structures act as accessory organs of adhesion. A view of the lunule and its relationship with the 1st antenna and with the anterior margin of the carapace is given in Fig. 29.

The 1st Antenna (Fig. 15, 17–21, 24–29)

The 1st antenna is 2-segmented. It is worth mentioning that Wilson (1905) and others believed that the frontal plates are modifications of the basal segments of the 1st antennae. Although this view, on the basis of embryological evidence (Heegaard, 1947) and articulation, is unacceptable, it is clear that the basal segments of the 1st antennal and the frontal plates together form a structural complex on the anterior margin of the cephalothorax (Fig. 29) which assists the parasite in maintaining contact with its host. The general compression of the body of *Caligus* has been followed by similar compression of the broad basal part of the 1st antenna. Roughly quadrangular in dorsal and ventral views (Fig. 24, 25), this part is quite flat and shaped to fit the overlying frontal plate (Fig. 19). This aspect of the basal segment structure can be seen in Fig. 27 and 28, displaying its posterior and anterior margins, respectively. A complex articulating surface joins the base of the 1st antenna with the anterior margin of the carapace (Fig. 24, 27, 28). Distally, the anterior margin of the basal segment is armed with numerous setae, fairly short and robust. The number of setae appears to vary from one specimen to another, but is usually 26 or 27. These setae are attached to the margin and, for some distance from it, to the ventral surface of the limb, with the exception of two setae (*ds*, Fig. 25) arising from the dorsal side of the margin. All but two of these setae are pilose.[4] These two setae (*ns*, Fig. 24, 25), near the border of the basal part, differ from the remaining ones only by being naked.

The distal segment of the 1st antenna is cylindrical (Fig. 24, 25). It is armed with naked setae only. One such seta, long and slender, is situated near the centre of the posterior margin of the segment. The blunt, rounded tip carries 13 setae arranged in two groups. The anterior surface of the tip is armed with eight shorter and stronger setae (seven only visible in Fig. 25), whereas the posterior surface is occupied by five setae, much longer and more slender than the above. Two of these setae arise from a common base, but divide very close to the tip of the antenna (*cb*, Fig. 26).

The 2nd Antenna (Fig. 30–37)

The 2nd antenna is distinctly different in the two sexes, that of the male having a much more complicated structure. These structural differences are related to the functions which

[4]We have distinguished between two types of setae which bear secondary setules. Where the secondary setules are arranged in two opposite rows the term *pinnate* is used. Where the setules are irregularly arranged we use the term *pilose*.

this limb performs. In the female the 2nd antenna is mainly an organ of prehension, assisting in the maintenance of the parasite's hold on its host, whereas in the male it also is used in grasping the female during copulation.

The 2nd antenna of the female (Fig. 30–34) appears 3-segmented. Wilson (1908) believed it to consist of 2 segments only. The basal segment, which is the shortest, is subcylindrical and armed with a backwardly projecting, fairly long, sharp-pointed outgrowth (*b*, Fig. 30–34). This is the vestigial exopod according to Heegaard (1947). The 2nd segment is the most robust of the three, accommodating most of the muscles controlling the movements of the claw. When in situ, the middle segment is deflected laterally to the base of the limb. On the dorsal surface of this segment (in retracted position) there is a small, finely grooved, lobe. This outgrowth (*ap*, Fig. 33) corresponds to the adhesion pads found on the same segment in the male. The claw of the antenna (*cla*, Fig. 30–34) is a hooklike structure. The sharply curved hamulus is provided with two naked setae. One of them is found on the inner margin of the claw near the base, at the tip of a small swelling; the other one occurs at about halfway from the base and is usually smaller. It is worth noting that in the vicinity of the 2nd seta the surface of the claw is marked by a definite transverse line, which appears to indicate some boundary of structure. This is likely the remnant of an articulation lost with the fusion of the two distal elements to form the claw at the end of larval development (Heegaard, 1947; Lewis, 1963).

As mentioned previously, the antenna can be folded away and tucked into a groove, posteriorly bounded by a slightly inflated margin, consisting of two poorly defined tubercles (*t*, Fig. 31).

The male 2nd antenna (Fig. 35–37) differs from that of the female to a considerable extent. Its basal segment is much longer and devoid of the sharp-pointed outgrowth. When in situ, it folds inwards from its point of articulation with the ventral surface of the body. It is irregularly cylindrical, but wider distally than at the base (*b*, Fig. 36). The middle segment is the most powerful segment of the limb. Its most characteristic feature is the presence of the adhesion pads (*ap*, Fig. 35–37). There are two of these structures on the surface of the middle segment. One is quite small and covers the surface of the segment at the point where one of the prongs of the claw touches when flexed (Fig. 35–37). The other is very large, wrapping around $\frac{3}{4}$ of the segment's circumference. The pads are raised above the surface of the segment and covered with numerous fine ridges, running mainly (though not exclusively) parallel to one another. When in situ, the 2nd segment is folded back over the 1st, so that its apical end is lateral and more or less over the base of the limb. The 3rd segment of the limb, the claw, is again reflected roughly in the opposite direction. The claw of the male 2nd antenna is of complicated structure. Its full extent is shown in Fig. 35. The tip of the claw is forked, consisting of two diverging, robust tines (*cla*, Fig. 35–37). Another and smaller structure, a seta borne at the tip of a small cone (*se*, Fig. 35–37), occurs subterminally on the inner surface of the claw.

The Postantennal Process (Fig. 4, 7, 30, 31, 52, 53)

The exact nature and homology of the postantennal process (Lewis, 1963) is still a subject for debate. It is a 1-segmented, strong, hooklike process arising from the ventral surface of the cephalothorax posterolateral to the base of the 2nd antenna. The convex side of the hook faces the lateral margins, and the concave is turned towards the centre of the body. On the expanded base of the hook are two setiferous papillae (*pa*, Fig. 52, 53). These papillae bear setules which superficially resemble the setules of the *a* type, found on the dorsal surface of the body but in reality are groups of much longer, unbranched, hairlike structures, arising from a common base, as shown in Fig. 52. Another such papilla is found on the ventral surface of the body, near to the base of the postantennal process. The number of hairlike setules is not constant. A cross-section through the papilla (Fig. 53) shows it to be a tight-fitting collar around the base of the setules. Under the papilla, the cuticle of the carapace is perforated by a funnel-like lacuna, with a nerve strand ending at its margins.

The Mouth Tube (Fig. 38–51, 54)

The mouth tube is situated in the centre of the ventral surface of the cephalic region of the cephalothorax. In general appearance (ventral view, Fig. 54) it is a short tube, broader at

the base than at the tip, which points obliquely backwards, away from the ventral surface. The tip of the tube is split in coronal plane and provided with a rim of narrow, striated membrane. The structure of the tube is that of a double-walled cylinder. The buccal cavity, delimited by the inner wall of that cylinder, is shown in cross-sections (Fig. 39–50, oriented with ventral side toward bottom of figure) cut at levels shown in Fig. 38. Anteriorly, this cavity is produced into two lateral, transversely flat ingrowths or horns (Fig. 39, 40) extending into the body cavity. To the tips of these horns are attached muscles which, by contracting, bend the basal part of the cavity and effect its complete closure at that end. The manner in which this can be done is best appreciated by reference to Fig. 51 in which the opening to the oesophagus (*oe*) is illustrated. The flat basal part of the buccal cavity soon expands into the cylindrical part, as seen in Fig. 43. Quite close to the base of the tube, on its lateral surfaces nearest to the bases of the mandibles, the outer wall of the tube is indented. The indentation is already noticeable in Fig. 43, and a little farther distally it has become a semienclosed duct, housing the mandibular shaft. The duct obliquely traverses the space between the inner and outer wall of the tube and not far from the middle of the tube penetrates the buccal cavity, and admits into it the distal part of the mandible. Distal to the point of penetration the tube remains split into dorsal and ventral lips (Fig. 46, 51, 54). Externally, the point of penetration is marked by a slight lateral notch in the surface of the tube.

Figure 54 shows that the dorsal lip is broad at the base. Laterally it is equipped with a raised margin which serves as a guide for the mandible. It is inside this guide that the mandible can move. The distal half of the ventral lip curves on its sides into thin flaps, protecting the longitudinal slit between the lips (Fig. 49). Its tip is slightly raised and forms a rooflike outgrowth, fringed with a membrane (Fig. 54). The important feature of the dorsal lip is the presence in it of two long and narrow depressions, which house the distal parts of the mandibles (Fig. 50).

The ventral component of the tube is much thicker than the dorsal component. It contains numerous bands of muscles within it, so arranged as to be capable of pulling together the inner and the outer wall of the tube.

The Mandible (Fig. 55, 56)

As mentioned above, this appendage arises lateral to the mouth tube and penetrates the buccal cavity. A mandible consists of four parts, possibly corresponding to four segments. The basal ¾ of the limb is circular in cross-section, as can be seen in sections (Fig. 44–48). The basal part is widest and gradually tapers towards its distal end. The 2nd part is very short and cylindrical. The 3rd part provides the main shaft of the appendage. The distal end of this part enlarges near its tip, where it fuses rigidly with the terminal part. The terminal part is bladelike, one of its margins being smooth resembling a knife, the other serrated in the form of a saw with 12 teeth, all curving in basal direction and of more or less uniform size and shape. This series of teeth does not lie in the same plane as the long diameter of the flat dentiferous part, but deflects from it at an angle of up to 45° towards the buccal cavity. The distal part of the mandible curves along the inner contour of the mouth tube, which at this point decreases in diameter to the buccal orifice. It is not generally realized that the retracted position of the mandible in the mouth tube is along the roof of the buccal cavity, with dentiferous margin of the limb *towards* the cavity, i.e. ventral (Fig. 51).

The Postoral Process (Fig. 4, 7, 30–32, 54, 57–59)

Like the postantennal process, the postoral process (Lewis, 1963) is still the object of disagreement, its homology and nature not being fully understood. The postoral process has been considered as the 1st maxilla (Gurney, 1933) and as the 2nd maxilla (Heegaard, 1947). Each postoral process is situated posterolaterally to the mouth cone. It consists of a broad-based tubercle tapering into a heavy spine with the tip pointing posteroventrally and extending beyond the tip of the mouth cone. Immediately anterior to the base of the process is a single papilla (*pa*, Fig. 57, 58) carrying three flattened, naked setae of unequal length. Sections through the region of the postoral process show that both the process itself (*pop*, Fig. 59) and the neighbouring

papilla are hollow outgrowths of the ventral surface of the carapace. There are no traces of articulation.

The Maxilla (Fig. 60–64)

The bases of the maxilla are posterolateral to the postoral process. The maxilla is of the same structure in both sexes. It is usually considered to be 2-segmented (Lewis, 1963). The two segments articulate upon each other in a manner resembling the human arm (Fig. 62, 63), the joint between them corresponding in position to the elbow. The unarmed basal segment is the more robust and shorter. The distal segment provides the main shaft of the limb. It is about 1.5 times as long as the basal segment. On its anterodorsal aspect, in the distal half of the segment, there is a small membranous flap (*f*, Fig. 60, 61), which is seen better in the dorsal aspect of the limb (Fig. 61, 63). The segment narrows rapidly toward its distal end. At the end are two long, tapered, gently curved, spinelike extensions, one of them terminal and the other subterminal. The terminal "spine" is longer than the subterminal extension and a suture apparently exists between it and the terminal segment. At four points around its circumference (dividing it into four more-or-less equal sectors) are attached very fine, serrated membranes, which run almost the whole length of the structure and are very difficult to observe in detail. A closer view of these membranes is shown in Fig. 64. The subterminal extension resembles the terminal spine quite closely, except for its shorter length, the apparent absence of a suture, and for the fact that it is equipped with only two strips of serrated membrane.

The Maxilliped (Fig. 65–72)

The size and the structure of this subchelate limb suggests that it is the main prehensile appendage of the parasite. As such, it is endowed with a wide range of mobility. Consequently, the collection of specimens examined displays the maxilliped in many different postures and one finds it rather difficult to define various aspects when describing this appendage. In this description it will be assumed that the maxilliped is flat against the body, as shown in Fig. 7, its tip pointing medially in the flexed position. Reference terms such as dorsal, ventral, lateral, and medial are to be understood as applied to the limb in this posture (Fig. 67).

The maxilliped of the female (Fig. 65, 67) differs in details of armature and in the relative proportions of the component parts from that of the male (Fig. 69–72), but the basic structural plans are the same. The limb of both sexes essentially consists of two articulating parts: proximal and distal. The latter ends as a fairly short, curved, and sharply tapered claw. A suture line at the base of this claw suggests the distal part may be derived as a fusion of penultimate and ultimate elements, although embryological evidence is lacking. A small auxilliary spine (*aux*, Fig. 65, 67, 68) is present at the base of the claw.

The female maxilliped is distinguished by the slenderness of the basal part. This part, in the shape of an elongated oval, is unarmed except for the presence of a small swelling (*pa*, Fig. 66–68) on the anterior margin against which the claw presses when the limb is flexed.

The male maxilliped is characterized by the strength and size of its basal part. The relative width of this part is more than twice that of the female limb. The armature of the anterior margin consists of two fairly regular, conical tubercles with sharp tips. It is between the tips of these tubercles that the tip of the claw is nested when the limb is flexed. In Fig. 69 and 70 these tubercles are referred to as the proximal tubercle (*pt*) and distal tubercles (*dt*) respectively. The tip of the claw abuts on the base of the proximal tubercle, which has near its base an additional outgrowth, visible from the ventral aspect (Fig. 70). The distal tubercle is more regular in shape and somewhat smaller. Its tip bisects the space enclosed by the claw and the anterior margin of the basal segment. The claw of the male limb is characterized by a relatively smaller auxiliary spine than that of the female.

The maxilliped of a juvenile male (Fig. 68) appears intermediate between that of the female and of the adult male. It resembles the female by the absence of elaborate armament on the basal part and is reminiscent of the male in the broader and more robust basal part. The tip of the juvenile maxilliped rests, when closed, on a swelling much more pronounced than that of the female limb, but resembling it more than that of the male.

The Sternal Furca (Fig. 73–77)

The homology and the function of this appendage is still being debated (Lewis, 1966). Although it has been illustrated by many workers and in many caligid species, its structure has never been satisfactorily understood and presented. In *C. curtus* (and presumably in other species of *Caligus*) the sternal furca is basically an elongated cylinder of heavy cuticle. The posterolateral sides of the cylinder grow out into two hollow, digitiform structures slightly divergent and with broadly rounded tips. These outgrowths form the tines of the sternal furca. At the anterolateral corners of the cylinder the lateral walls produce a pair of ingrowths (*h*, Fig. 73, 75–77) which extend dorsally into the body cavity. Powerful longitudinal muscles, originating from the sternum posterior to the 1st interpodal bar, are attached to the tips of these ingrowths. A smaller pair of muscles, originating anterodorsally within the body cavity, are attached to the bases of the ingrowths. The entire rim of the cylinder, lateral to the ingrowths, is connected to the ventral carapace by a ring of thinner, flexible cuticle. The longitudinal muscles are capable, by contraction, of erecting the entire cylinder in relation to the ventral body surface, thus elevating the tines of the furca. Contraction of the anterodorsal muscles prevents posterior movement of the entire structure, their points of insertion being at the axis of rotation.

Thoracic Appendages

In the following discussion of thoracic appendages, again the terms medial, lateral, dorsal, and ventral refer to orientation with the main body axis and the limb is understood to be in the position as shown in Fig. 4 and 7. It should be mentioned here that the interpodal bars were considered by Pedashenko (1898) to be derived from the coxopodite of the protopods. We have not examined this proposition but, at the present time, for descriptive purposes, prefer to treat them as structures distinctive from the thoracopods.

The 1st Thoracopod (Fig. 78–81)

The 1st pair of thoracic legs are connected by an interpodal bar (*ipb*, Fig. 80, 82). The 1st interpodal bar is a tube of heavy cuticle, nearly circular in cross-section (Fig. 82) and attached to the ventral surface of the body by its anterior margin. At least $\frac{3}{4}$ of the tube's circumference is free, and the attachment is flexible so that the bar can be rotated through a considerable arc around its longitudinal axis. At both ends, where the bar joins the protopods, it enlarges and its shape is moulded to allow articulation with the legs (Fig. 80).

The protopod is 2-segmented. The two segments overlap each other in such a fashion that, when seen in the ventral aspect, the distal segment (*pr* 2, Fig. 80) almost completely covers the basal (*pr* 1, Fig. 80). The basal segment, which is dorsal to the distal, is also more anterior. This arrangement, when seen ventrally (Fig. 4, 7), gives an impression that the protopod is a single segment. The line of division between the segments is best observed in posterior view (Fig. 80). The posterior aspect of the protopod bears a fine groove, which in some specimens is accentuated to produce a distinct cleft along the surface of the protopod. The basal segment is armed only with a small papilla, bearing two fine setules (*se*, Fig. 78, 79). The distal segment has on its posterior margin a small pinnate seta. Another similar but smaller seta is carried near the border of the exopod, on the anterior margin. This seta is better seen from the ventral aspect of the limb (Fig. 78).

The endopod has been reduced to a small, unsegmented papilla (*en*, Fig. 78–80).

The exopod consists of two segments (*ex*, Fig. 78, 79). The proximal segment is much larger than the distal one. It is long and narrow, armed with a fringe of short hairs along its posterior margin and bears a single naked spinule on the anterior margin, near the junction with the distal segment. The latter segment is shorter and narrower than the proximal segment. Its anterior margin is unarmed. The posterior margin bears three long pinnate setae. The lateral margin (the tip of the distal segment) is armed with four setae of completely different type (Fig. 81). The one nearest to the three long, pinnate setae is the longest of the four. It is slender, smooth, and tapers towards the tip which bears a distinctly delimited, pinlike protrusion. The other

three structures, all of about the same length, are shorter and more robust than the first. They are dactyliform with rounded and blunt ends which, however, also bear clearly demarcated, fine points. The tips of these three structures, around the bases of the points, are beset with fine denticles which also extend some distance proximally, particularly along the lateral margins of the setae. The most lateral of these seta bears these denticles for more than ½ its length distally.

THE 2ND THORACOPOD (FIG. 83–90)

In the same way as the preceding pair of appendages, the legs of the 2nd pair are joined by an interpodal bar. The bar of the 2nd pair differs from that of the 1st in several respects. It is not circular in cross-section but rather pyriform, with a narrow, peduncular base (*ipb* 2, Fig. 82). The anterior margin of the bar attached to the ventral surface of the body, though of nearly the same absolute extent as that of the first bar, constitutes only a small portion of the bar's surface. The posterior margin of the bar is provided with a strip of transparent membrane (*m*, Fig. 82, 83), which is widest in the centre and narrows laterally.

The protopod of the 2nd leg is 2-segmented, its two segments being arranged essentially in the same way as those of the 1st leg. The proximal segment is dorsal in relation to the distal. Seen in ventral aspect, the proximal segment appears to have slipped from under the distal, not only in anterior direction, but also in medial. There is, therefore, an appearance of two segments, a short proximal and a larger distal. An anterior view of the limb (Fig. 85) shows clearly, however, that these two segments are not linked to each other "end to end," but that the proximal segment (*pr* 1) extends over a large area of the dorsal surface of the distal segment (*pr* 2). It shows also that the long axes of these two segments are at an acute angle to each other. On the ventral, exposed surface of the proximal segment there is a short and naked seta (*s* 1, Fig. 83, 86). On the posterior margin of the segment, in the space between the interpodal bar and the second segment, there is a large, pinnate seta. The anterior margin of the proximal segment carries, at its lateral corner, a small flap of transparent, striated membrane (*m* 1, Fig. 84, 85), reflected posteriorly along the dorsal surface of the limb. The distal segment of the protopod is armed with two naked setae which can be best observed in the ventral view of the limb (Fig. 83). One of them (*s* 2) is quite small, situated at about ⅓ of the segment's length from the medial limit near the posterior margin; the other (*s* 3) which is more aptly described as a small spinule, can be seen in the lateral corner of the anterior margin near the junction with the exopod. A strip of transparent membrane is present along the entire posterior margin of this segment.

The exopod is 3-segmented. The 1st segment provides about half the length of the ramus. At the distolateral corner is a powerful spine which, in situ, extends obliquely to the centre of the terminal segment of the ramus along its ventral surface. This spine narrows abruptly at about ⅓ of its length from the broad base. From that level, right up to the finely tapered tip, the opposite margins of the spine are rimmed with strips of very narrow, transparent membrane. Close to the base of the spine the lateral margin also carries a small, fine setule. At the distomedial corner, the segment is equipped with a long, pinnate seta. However, the most striking feature of this segment is the presence on its lateral margin of a large membrane, similar to that carried by the basal segment of the protopod but much larger. This membrane (*m* 2, Fig. 84, 85) extends as a posteriorly directed flap along the dorsal surface of the limb, covering the base of the endopod, and almost the entire exopod with the exception of the tip of the terminal segment. The 2nd segment is short and almost square, and carries at its distolateral corner a medium-size spine. This spine (Fig. 87) has on its ventromedial surface a coarsely striated flange with serrated margin. (In Fig. 87 the 3rd segment has been detached for the sake of clarity.) This spine extends to the 3rd segment and, in ventral view, is often obscured by the large spine of the 1st segment. Distally, on the medial margin of the segment, one large pinnate seta is present. The 3rd segment of the exopod is rounded in outline. Along the medial edge and around to the distal tip, the margin is occupied by five long, pinnate setae. Continuing around the margin (Fig. 83, 84) there are three more structures, shown in detail in Fig. 88–90. The 1st, situated proximally on the lateral margin, is the smallest and carries two rows of serrations. This spinule appears to be capable of some movement around its longitudinal axis so that one of these rows can be hidden from view, as

in Fig. 88. Both rows are clearly visible in Fig. 89. Distal to the spinule is a much larger, robust spine (Fig. 88, 90) which is somewhat variable in shape among specimens. Its tip often curves and its ventromedial surface, like that of the spine of the 2nd segment, is equipped with a thickened broad flange which narrows toward the tip (Fig. 90). The margin of this flange is serrated.

It is worth noting that the flanges of the spines on the 2nd and 3rd segment clearly differ from the two membranes carried by the spine of the 1st segment. In the latter the membranes are finely striated, with even and entire margins. The flanges, in contrast, are coarse and uneven. An impression is created that the flanges of the spines on the 2nd and 3rd segments have originated from the multiple rows of separate setules, which have fused more or less completely. The degree of fusion seems to vary from one specimen to the next. On the other hand, the membranes of the 1st segment's seem to have been produced as extensions of the spine margins. Next to the 1st of the five long, pinnate setae there is the last element of the armament of this segment. This is a medium-length seta, with a single row of setules along its medial margin and a very narrow strip of membrane along the lateral edge (Fig. 88).

The endopod is also 3-segmented (Fig. 83, 84). The basal segment of this ramus has margins of uneven length; the lateral margin is much longer than the medial one and curves to produce a "knee," which displaces the ramus medially and makes it diverge from the laterally protruding exopod. This knee is provided with a dense patch of setules. The short medial margin carries one long, pinnate seta. The lateral margin of the 2nd segment is fringed with setules which, however, are shorter and not as heavy as those of the 1st segment. Its medial margin carries two long, pinnate setae. The 3rd segment is small, with a rounded outline armed with six large, pinnate setae, increasing in length from lateral to medial.

The 3rd Thoracopod (Fig. 92–96)

This pair of thoracopods has been greatly modified and forms an apron which completes posteriorly the ventral concavity formed by the cephalothorax and its marginal membranes. Modification has been achieved mainly by structural changes of the interpodal bar and the protopod. The rami, which have become divorced from a primary function of locomotion, are greatly reduced. The width of the interpodal bar can be seen clearly in Fig. 4 and 7. A cross-section through it (Fig. 92) shows its double-walled structure, with trabeculae of tissue joining the opposite walls and the short marginal membrane being present on the posterior margin.

The segments of the protopod have become fused to the extent that it is no longer possible to distinguish between them. We suggest, however, that a major part of the ventral surface of the limb (Fig. 96) represents the 2nd segment, whereas the 1st segment contributes mainly to the formation of the dorsal surface (Fig. 94, 95). The central part of the dorsal surface (*c*, Fig. 94) can be seen as a bulge ending posteriorly in a sharp, crescentic line. It is possible that this line forms a part of the border between the 1st and 2nd segments, particularly in view of the fact that the rami which would naturally articulate with the 2nd segment are attached posteriorly to this line. It is worth noting that the thickness of the protopod decreases greatly behind this line to form a thin shelf capable of accommodating the entire, reduced exopod, if the latter were swung in medially. In some specimens the exopod was precisely in this position and in Fig. 95 it can be seen partly retracted. The margin of the protopod runs in a broad arc from the lateral to the medial end. The anterior ends of the lateral portion of the margin, seen in ventral view, carry a ridgelike adhesive pad (*ap*, Fig. 94, 96). This ridge leaves the margin and continues to run along the dorsal surface of the limb. It gradually diminishes in prominence and disappears a short distance from the beginning of the crescentic line mentioned above. A marginal membrane extends from the point where the ridge leaves the margin to the base of the exopod. This membrane is fairly broad and faintly striated. Directly at the base of the exopod there is a short, pinnate seta (Fig. 94). On the medial side of the endopod, the margin is also rimmed with a membrane, which extends to the junction of the protopod with the apron. Close to this junction, there is a long, pinnate seta. In addition, on the ventral surface of this area, close to the margin, there are two small naked setae, one near the base of the endopod and the other in the medial corner of the limb.

The exopod (*ex*, Fig. 94–96) is 3-segmented. The basal segment of the exopod is quite small and serves as the base for a powerful, slightly curved spine (Fig. 96) which extends over the ventral surface of the ramus, reaching the centre of the 2nd segment. This spine has a very narrow membrane on the lateral margin. A similar membrane on the medial margin could not be seen in all specimens examined. Just anterior to the base of this spine, the lateral margin of the segment also carries two minute naked setae (Fig. 94). The medial margin of the segment appears to have no armament. The 2nd segment is the largest one of the ramus, expanding in width from its base towards its junction with the 3rd segment. Its lateral margin is covered with a fringe of fairly long setules. On the distolateral corner, this segment bears a digitiform spine, which appears to consist of more than one part (Fig. 93). In addition to this spine two shorter spinules occur along the dorsal borderline between the 2nd and 3rd segments (Fig. 94). The distomedial margin of the 2nd segment carries one long, pinnate seta. The 3rd segment is the smallest of the three and is roughly semicircular. A fringe of hair-like setae is found on the lateral margin anterior to three short spines (Fig. 93) similar to that occurring at the distolateral corner of the preceding segment. These spines increase in size medially. Medial to them are four long, pinnate setae, also increasing in size in medial direction.

The endopod (*en*, Fig. 94–96) is also 3-segmented. The basal segment, which can be seen in dorsal aspect but is not evident in ventral, appears to be very small, serving only as the base for a single, long pinnate seta (Fig. 94). Careful examination shows, however, that the lateral margin of the segment, still retaining its continuity with the base, has extended into a long, oval platelike structure, the velum (*v*, Fig. 96). Lewis (1963) described the development of this structure in a species of a related genus (*Lepeophtheirus dissimulatus*). The velum fills the gap between the bases of the rami. Its free margin is fringed with hairlike setules, as it is in the corresponding segment of the 2nd leg. The anterior margin of the velum has fused with the protopod along most of its length, with the exception of the medial and the lateral extremities, which form rounded flaps. The 2nd segment is also expanded laterally into a thin plate bordered by a fringe of hairlike setules. This expansion is reminiscent of the development of the velum on the preceding segment. Two long pinnate setae are found on the medial margin of the 2nd segment. The suture between the 2nd and 3rd segments is very indistinct and in some specimens is very difficult to see. As in the 2nd leg, the 3rd segment is much smaller than the 2nd. It is armed with four long, pinnate setae, increasing in size from the lateral towards the medial side of the appendage.

The 4th Thoracopod (Fig. 97–100)

This limb bears little resemblance to the preceding three pairs of thoracopods. It is uniramous, consisting of a 1-segmented protopod and an apparently 2-segmented ramus. In its general structure, the 4th thoracopod bears some resemblance to the maxilla, being flexed in the manner of an arm. The protopod articulates with the ramus through an elbowlike joint.

The protopod is the strongest and the most muscular part of the limb. Its shape is irregularly oval (Fig. 97, 98). At the posterolateral corner, close to the junction with the ramus, it is armed with one small pinnate seta (*se*, Fig. 97, 98). In addition, a number of small naked setules (of the *b* type) occur along the lateral margin and on both dorsal and ventral surfaces near to the lateral margin of the protopod. The distribution of these setules is not constant, only few of them appearing in the same locations in different specimens. There are between 10 and 15 of them and some $\frac{2}{3}$ of that number are directly at the lateral margin.

The ramus consists of two segments with a weak oblique line of division between them. The laterodistal tip carries a short spine (*sp* 1, Fig. 97–100), which extends along the lateral margin of the distal segment to about the middle of its length. The lateral margin of the spine is fringed with a very deeply serrated membrane which resembles a series of very fine, transparent teeth and which is best seen in Fig. 99. At the base of this spine, on the ventral surface, there is a row of minute partly fused setules. The distal segment is longer than the proximal, and the distal margin slopes obliquely, its angled tip being the apex of the segment. This margin carries three spines, two of which are of a size similar to the spine of the proximal segment. The main difference between these and the spine of the proximal segment is the presence on one of their margins (opposite to the serrated membrane) of additional armament. This armament consists of

a short strip of similar serrated membrane in the basal half of the spine, followed by a row of fine denticulations, especially well seen in the larger of the two spines in Fig. 99. This armament is less well developed on the smaller spine and the extent of its development varies from one specimen to another. The laterodistal corner is occupied by the largest of the three spines, exceeding in length the larger of the remaining two by more than three times. Curved in its distal half and tapering to a fairly fine point, this spine has a row of distinct denticles along its dorsal surface. The denticles are largest at the middle of the spine and decrease in size proximally and distally. The denticles are well spaced out and peglike in the middle, but are closely packed and slender at the tip of the spine. Proximally, the row of denticles terminates at about $\frac{1}{3}$ of the spine's length from its base. At about that level the spine shows an abrupt difference in diameter (Fig. 100), sometimes giving an impression of a groove. A comblike structure, the pecten (*pp*, Fig. 99, 100) surrounds the medial aspect of the base of this spine. This structure consists of a semicircular flap of cuticle surrounded by a radially serrated membrane. Similar structures are present on the ventral surface of the bases of the smaller terminal spines (*pp*, Fig. 100), differing from the above-described in size only.

The 5th and the 6th Thoracopods (Fig. 11, 12, 91)

These two pairs of thoracopods, when present, are situated on the genital segment. Due to the difference in the development of the genital segment in the two sexes, the 5th and 6th thoracopods also differ to some extent.

In the female, the 5th leg has been reduced to two papillae, one carrying two, and the other one, short pilose setae. These papillae are situated near the lateral side of the lateral process (*lp*, Fig. 12). On the ventral surface of the genital segment, one can see also a medial process (*mp*, Fig. 12), which in our view is formed from the 6th segment and originally provided the site for the 6th thoracopod.

The male has both processes well developed (Fig. 11, 91). The lateral process, as described earlier, carries at its posterolateral corner the 5th thoracopod, which is represented by two cusplike protrusions, the dorsomedial carrying two and the ventrolateral carrying one pilose setae. The medial process is broad and flat, and often carries at its apex a naked spinule. The division between these processes is particularly well seen from the lateral side of the segment (Fig. 5 and 91). A deep cleft between the lateral and the medial process is strongly suggestive of their descent from the original two distinct components of the segment.

The Caudal Furca (*cl*, Fig. 2–7, 101)

The caudal furca consists of two caudal lamellae which, as mentioned earlier, are flat and roughly quadrangular. The medial margin of each lamella is covered with a fringe of fine hairlike setae. The fringe consists of several irregular rows and is heavier at both ends than at the centre of the margin. The lateral margins of the lamellae are unarmed, save for minute setules of type *b*. The distal margins carry six pinnate setae. Their relative sizes are best shown in Fig. 101. The centre of the margin is occupied by three long setae, while its extremes carry much smaller structures. There is one very small seta in the medial corner and, in the male, one at the lateral corner. Directly medial to the latter seta is a somewhat larger seta. In the female, the smaller, most-lateral seta is found on the ventral surface of the lamella, close to the base of the larger lateral seta, and projecting ventrally (Fig. 101).

DISCUSSION

Most parasitic copepods are comparatively small. Consequently, detailed study of their morphology is beset with many difficulties. As the result of these difficulties, many structural details have been misunderstood, others simply disregarded. A good example of this disregard is presented by the 1st antenna of *Caligus*. It is frequently described as carrying on its tip "a

few" setae, "a tuft" of setae, or "many" setae. One species, *C. polycanthi* Gnanamuthu, 1949, was given its name because it was believed to have particularly numerous (nine) setae at the tip of the 1st antenna. Some workers gave in their descriptions definite numbers, differing from 4 to 12. It has become apparent recently, however, that the number of setae at the tip of the 1st antenna of *Caligus* is constant. *Caligus curtus* is no exception. In common with its congeners, it has 13 setae on the tip of the 1st antenna, the size, shape, and position of these setae being constant. This fact has now been checked and described for *C. willungae* and *C. fortis* (cf. Kabata, 1965). On reexamination, the same number was found in *C. clemensi* Parker and Margolis, 1964; *C. zei* Norman and Scott, 1906; *C. gurnardi* Krøyer, 1863; *C. diaphanus* Nordmann, 1832; and *C. longicaudatus* Brady, 1899. Thirteen apical setae were also found in species studied of the genera *Dissonus*, *Mappates*, *Dentigryps*, *Heniochophilus*, and *Pseudanuretes*. It is fair to assume that the number is prevalent, perhaps constant, throughout the caligids and caligoids.

One of the facts which adds to the difficulty of studying the morphology of the parasitic copepods is the translucency which renders many internal structures visible and makes it difficult to decide whether the particular structure studied is superficial or not. This applies particularly to structures of some complexity, such as the mouth tube of *Caligus*. Many earlier workers, describing this tube, included in their illustrations elaborate systems of struts and bars, representing them as significant structural features. Some of these are no more than cuticular ridges, mainly internal, serving as structures supporting the working of the tube. Others are artifacts caused by viewing the transparent cuticle from the side, thus giving the impression of thickness. None, however, is seen externally and in this paper they have been purposely ignored. As stated in the description, the mouth tube is a double-walled tube, distally separated into dorsal and ventral components and containing a pair of mandibles, introduced by lateral involutions and slits. The mandibles, therefore, lie as ramrods in a cylinder, capable of being thrust into contact with host tissue and withdrawn.

On the basis of structure we are suggesting the following mode of operation of the mouth tube and mandibles. When feeding, the mouth tube is erected until it is placed at right angles to the surface of the host. The buccal cavity is then applied to this surface, the marginal membranes spreading around its circumference like a collar, maintaining a seal. The mandibles can then slide in and out within the cavity, the cutting blade of the distal margin macerating the tissue of the host and the teeth of the opposite dentiferous margin serving as a rake. The entire cavity can be shut off by the distal marginal membranes, by the flaps protecting the slits laterally, and by closing of the oesophageal orifice proximally by contraction of the muscles attached to the horns. The musculature of the thick ventral side of the tube can, by contraction, bring the inner wall of the cavity in apposition with the outer wall and in this way enlarge the cavity and create a partial vacuum within it. The particles of macerated host tissue are thus drawn toward the oesophagus. Relaxation of

the muscles in the ventral lip and opening of the oesophageal orifice forces the contents into the digestive tract of the parasite.

The method of suction is also used to effect the attachment of the parasite to its host. The ventral surface of the cephalothorax is applied to the host's surface, the marginal membranes, the frontal plates, and, posteriorly, the 3rd thoracopods, sealing it off from outside. The cup, thus formed, can then increase its volume and create the required suction. The method of creating the increase is not as yet understood. Wilson (1905) credits I. C. Thompson with suggesting that the body is raised from the host by erection of the sternal furca, though he rather thought of increasing the space for the facilitation of the work of other appendages, not for creating suction. However, in Wilson's (1905) view the sternal furca is used as a brake to prevent backward sliding of the animal. Heegaard (1947) believes that the erection of the furca cannot be used for the purpose suggested by Thompson, since the limbs occupy more space than can be provided by the furca. The necessary suction would then be produced by the arching of the carapace itself, caused by contraction of the well-developed musculature.

In connection with the above, it might be mentioned that the structure of the sternal furca has rarely been understood. In common with the mouth tube, its translucency made it difficult to interpret its true structure. Hence, only the thicker walls (anterior, posterior, and lateral) usually have been illustrated, in addition to the tines, resultjng in the all-too-familiar drawings of figures resembling the letters H or A. Reference to Fig. 73–77 makes the structure of the caligid sternal furca clear and its mode of operation more easily understandable. Whatever the purpose of this action, the furca can be erected so as to assume a position with tines almost at right angles to the surface of the host.

The examination of the thoracic legs of *C. curtus* has also provided interesting information. This has been summarized in Fig. 102–104. In spite of the modification and diversification of structure undergone by the thoracic legs of *C. curtus*, their homology can still be traced to a considerable extent. One of the unexpected discoveries in the course of this study was that of the 2-segmented character of the 1st protopod. There is no reason why this should not have been suspected, since the primitive condition in the copepods, including the free-living species, is usually a 2- or perhaps 3-segmented protopod. The study of the development of *C. curtus* (cf. Heegaard, 1947) did not reveal the presence of two segments in the 1st protopod at any stage. This is probably due to the "overlap" arrangement of the two segments in this genus.

The homology of the exopod is fairly simple. The terminal segment is obviously the same in all three pairs of thoracopods compared. It is impossible to decide whether the 1st or 2nd segment has been suppressed in the 1st thoracopod but these two segments are clearly identifiable in the 2nd and 3rd thoracopods. As regards the endopods, comparison was restricted to the 2nd and the 3rd thoracopods, since that of the 1st thoracopod has been reduced to a mere vestige. Associated with the complete functional change of the

3rd thoracopod, its endopod has undergone a remarkable modification. The first segment has extended to produce the velum, reaching all the way to the now fairly distant exopod. As can be seen in Fig. 103 and 104, this extension did not lose the original margin of setules present in the 2nd thoracopod as it is also present on the velum. The homology of the remaining two segments is also clear from the diagram.

The determination of the homology of the 3rd thoracopod's protopod is most difficult. It has been argued earlier (Heegaard, 1947) that the flat expanse of this part of the leg was composed of two component segments. Heegaard, however, does not make clear the arrangement of the two segments in the adult protopod.

In the light of the present study it seems clear that both segments contribute to the formation of both surfaces of the limb, but that the distal segment, as in the 1st two thoracopods, is mainly responsible for the ventral surface. The posteromedial corner carries the landmarks of both the proximal and the distal segments. The long, pinnate seta belongs to the proximal, whereas the marginal membrane (*x*) and one of the accompanying setae belong to the distal segment. The lateral margin of the protopod also carries the landmarks of both segments: the long marginal membrane (*y*), homologous with the short one found on the 2nd leg on the proximal segment, and a short seta, present near the base of the exopod on the distal segment.

All these comparisons exclude the 4th thoracopod because the latter has evolved under circumstances differing from those of the preceding thoracopods. The 4th thoracopod has become functionally divorced from the preceding appendages by being excluded from the set contained under the carapace. This exclusion arose with the development of the barrier formed by the modification of the 3rd thoracopods. The 4th thoracopod, therefore, has assumed an entirely different functional role, and its evolution has obscured analogy with the other thoracopods.

The improvement of the celphalothorax as an efficient suction cup is a specialized feature absent from the more primitive genera of caligoids. A very illuminating example of the primitive caligoid condition is shown by the genus *Dissonus* (cf. Kabata, 1966). Superficially resembling *Caligus*, the genus *Dissonus* shows its primitive nature in the fact that two fewer thoracic segments have been included into the cephalothorax than in *Caligus*. It is interesting to compare the thoracopods of the two genera. The 1st thoracopods of these parasites differ mainly by the presence of a much better developed endopod in *Dissonus*. Its small size, however, heralds the future trend towards complete reduction. It is also clear that in both genera the 1st thoracopod is not as well developed as the 2nd and it seems that the 1st does not take a great part in the function of locomotion. The 2nd thoracopods of *Caligus* and of *Dissonus* are very similar to each other, both in general structure and in the armature. *Dissonus* differs only in having fewer modified setae and more typical long, pinnate setae. The endopods are virtually identical. A difference between the two genera appears clearly in the 3rd thoracopod.

Whereas in *Dissonus* the 3rd thoracopod differs from the 2nd only in some details of the armature, in *Caligus* it has become extensively modified. The consequences for the 4th pair are clear. In *Dissonus* this pair resembles both the 2nd and the 3rd, again differing from them only in details of armature. On the other hand, in *Caligus* the 4th thoracopod has become a simple, uniramous appendage.

Throughout the text we have referred to the presence of minute setules on the integument of *C. curtus*. There are three main types. As shown in Fig. 10, type *a* branches out from a single base, and type *b* is a simple unbranched setule. The latter may vary considerably in length. A short variety mainly occurs on the more exposed surfaces of the carapace, free thoracic segments, abdomen, and 4th thoracopods. Longer setules are usually found in association with the membranes rimming the carapace and on the first 3 pairs of thoracopods. The third, type *c*, consists of a bundle of 2–4 hairlike setules arising out of a common base. This type is illustrated in Fig. 52 and 53. These three types of setules have some common features. They are all very small, in fact minute. They arise from papillae which are supplied with nerve fibers (Fig. 53). From this structure it is inferred that these organs are sensory. It seems rather strange that they have not been reported from the genus *Caligus* more frequently. Pickering and Dana (1838) found them on *C. curtus*. With the exception of *C. sensilis* Kabata and Gusev, 1966, a species which has been established in part due to its possession of these sensory setules on the carapace, and *C. longicaudatus* Brady, 1899 (cf. Parker, 1968), no species has been described as having them. The authors believe that more careful examination will reveal their presence in many more, if not all, species of *Caligus*.

Particularly in the older literature, much has been made of the shape of the genital segment in describing and differentiating species. The shape of the genital segment in *C. curtus*, and in other members of the genus (Guibé, 1936), is quite plastic, depending on the state of maturity and, in females, the stage of egg laying. In Fig. 105 and 106, outlines are given of a small immature male and a large mature male, respectively. In Fig. 107, a small mature gravid female is shown which can be compared with a much larger postgravid female illustrated in Fig. 108. These specimens were selected from the same collection to illustrate developmental changes that occur to the relative size and shape of the genital segment.

A collection containing 28 females and 52 males was measured. The total lengths (including frontal plates and caudal lamellae but not membranes or setae) of the females ranged from 5.10 to 10.10 mm (average 8.77 mm) and of the males from 5.38 to 12.30 mm (average 7.93 mm). Although these statistics reflect the tendency for the females to be longer than the males, sexual dimorphism obscures the real relationship between male and female size when total length is used. Carapace lengths form a better basis for comparison of the sexes and also, being the largest single nontelescoping unit of the body, are taken as a "standard" length for comparing relative sizes of body parts. Carapace lengths (excluding frontal plates) of females and males

ranged from 2.50 to 4.88 mm (average 4.30 mm) and from 3.73 to 6.93 mm (average 4.38 mm), respectively. Thus the males averaged slightly larger in respect to carapace length and showed a larger maximum size. The main sexual dimorphism lies with the genital segment. Among the females the genital segment was between 27.5 and 69.2% (average 57.8%) of the length of the carapace. Among the males the length of the genital segment ranged from 19.5 to 40.4% (average 29.1%) of the carapace. Thus a large amount of variability can be expected in the body proportions of *C. curtus* and presumably in other members of the genus.

ACKNOWLEDGMENTS

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LIST OF ABBREVIATIONS

a — articulating process
abd — abdomen
ant 1 — 1st antenna
ant 2 — 2nd antenna
ant 1(*a*) — 1st segment of 1st antenna
ant 1(*b*) — 2nd segment of 1st antenna
ap — adhesion pad
ar — anterior region of carapace
aux — auxiliary spine
b — base
c — central part of the dorsal surface of the 3rd thoracopod
ca — cephalic area
cb — common base
cl — caudal lamella
cla — claw
dl — dorsal lip
ds — dorsal seta
dt — distal tubercle
e — eye
en — endopod
es — egg sac, or origin of egg sac
ex — exopod
ex 1 — 1st segment of exopod
ex 2 — 2nd segment of exopod
ex 3 — 3rd segment of exopod
f — flap
fp — frontal plate
g — groove
gs — genital segment
h — horn
ind — indentation
ipb — interpodal bar
ipb 1 — 1st interpodal bar
ipb 2 — 2nd interpodal bar
l — lunule
la — lateral area
lp — lateral process
m — membrane
m 1 — membrane of protopod of 2nd thoracopod
m 2 — membrane of 1st segment of exopod of 2nd thoracopod
mc — mouth cone
mdb — mandible
mm — marginal membrane
mn — marginal notch
mp — medial process
ms — middle segment
mx — maxilla
mxp — maxilliped
ns — naked seta
oe — oesophagous
pa — papilla
pp — pectinated plate
pap — postantennal process
pcr — posterior cephalic ridge
pop — postoral process
por — posterior ridge
pr — protopod
pr 1 — 1st segment of protopod
pr 2 — 2nd segment of protopod
ps — posterior sinus
pt — proximal tubercle
s — swelling
s 1 — spinule 1
s 2 — spinule 2
sc — sensory crypt
se — seta, setule
sf — sternal furca
sp 1 — 1st spine
t — tubercle
ta — thoracic area
th 1 — 1st thoracopod
th 2 — 2nd thoracopod
th 3 — 3rd thoracopod
th 4 — 4th thoracopod
th 5 — 5th thoracopod
th 6 — 6th thoracopod
v — velum
vl — ventral lip
x — membrane of 1st segment of protopod
y — membrane of 2nd segment of protopod

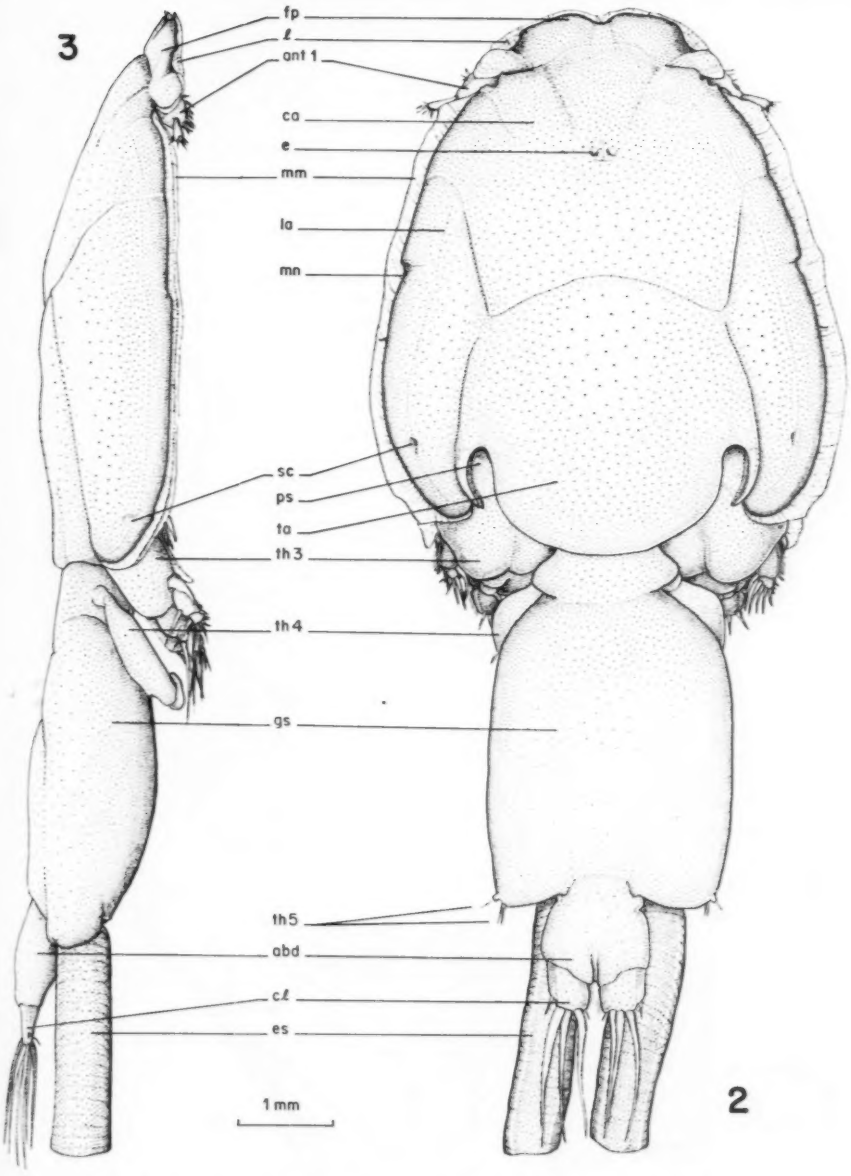
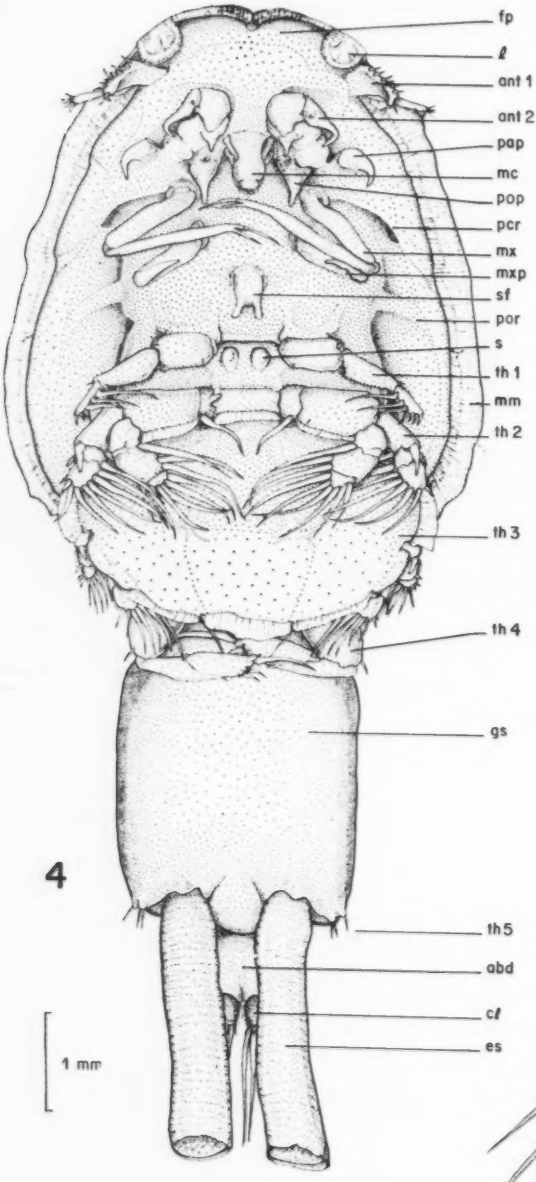


FIG. 2. Female, entire, dorsal. FIG. 3. Female, entire, lateral.



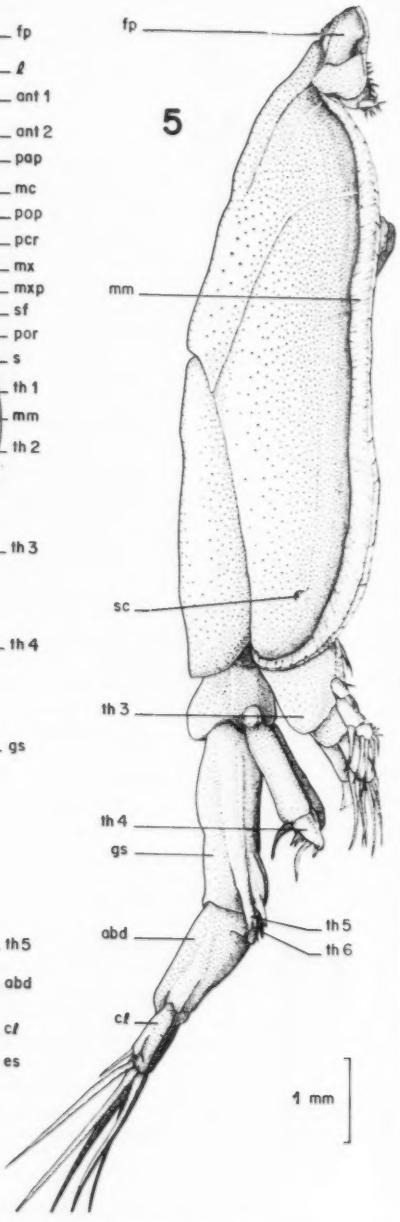


FIG. 4. Female, entire, ventral. FIG. 5. Male, entire, lateral.

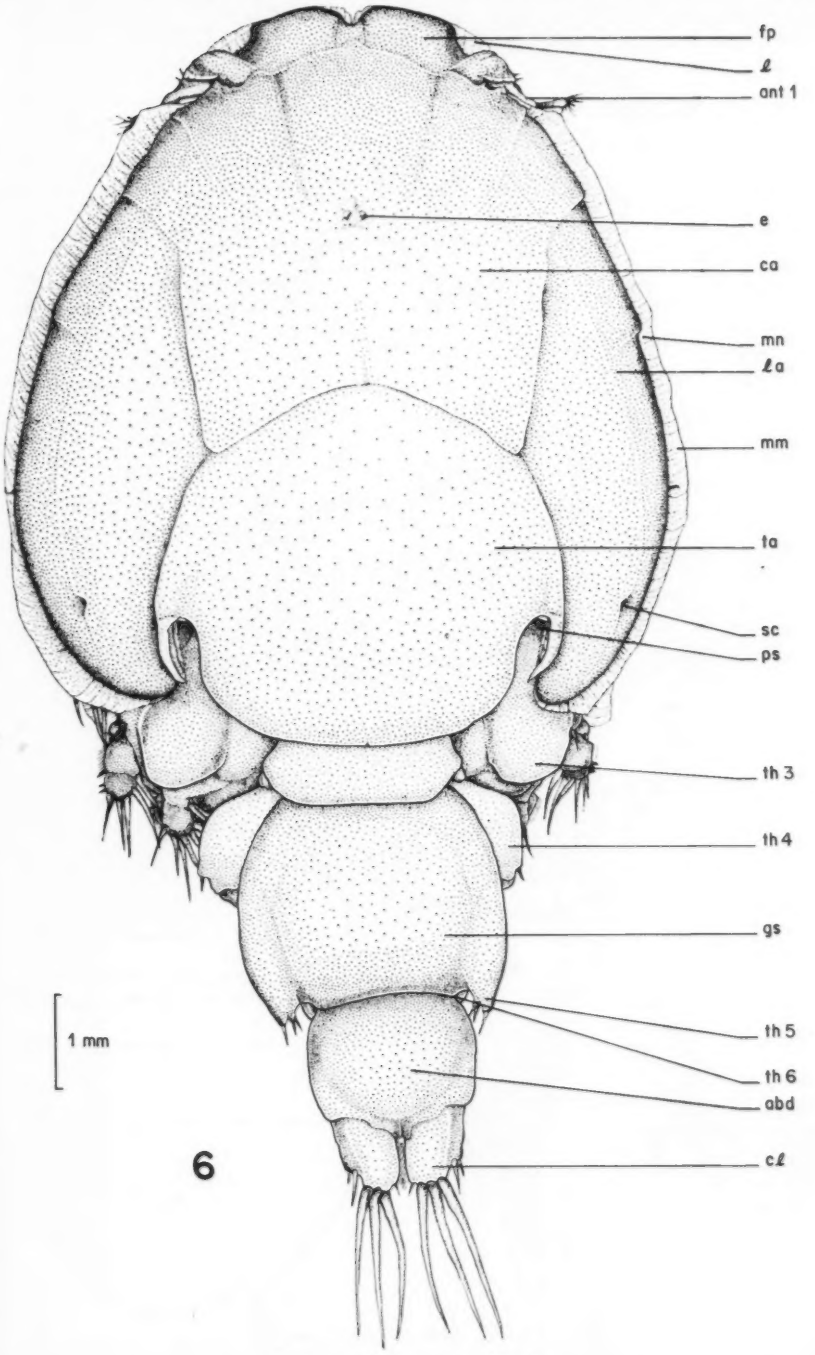


FIG. 6. Male, entire, dorsal.

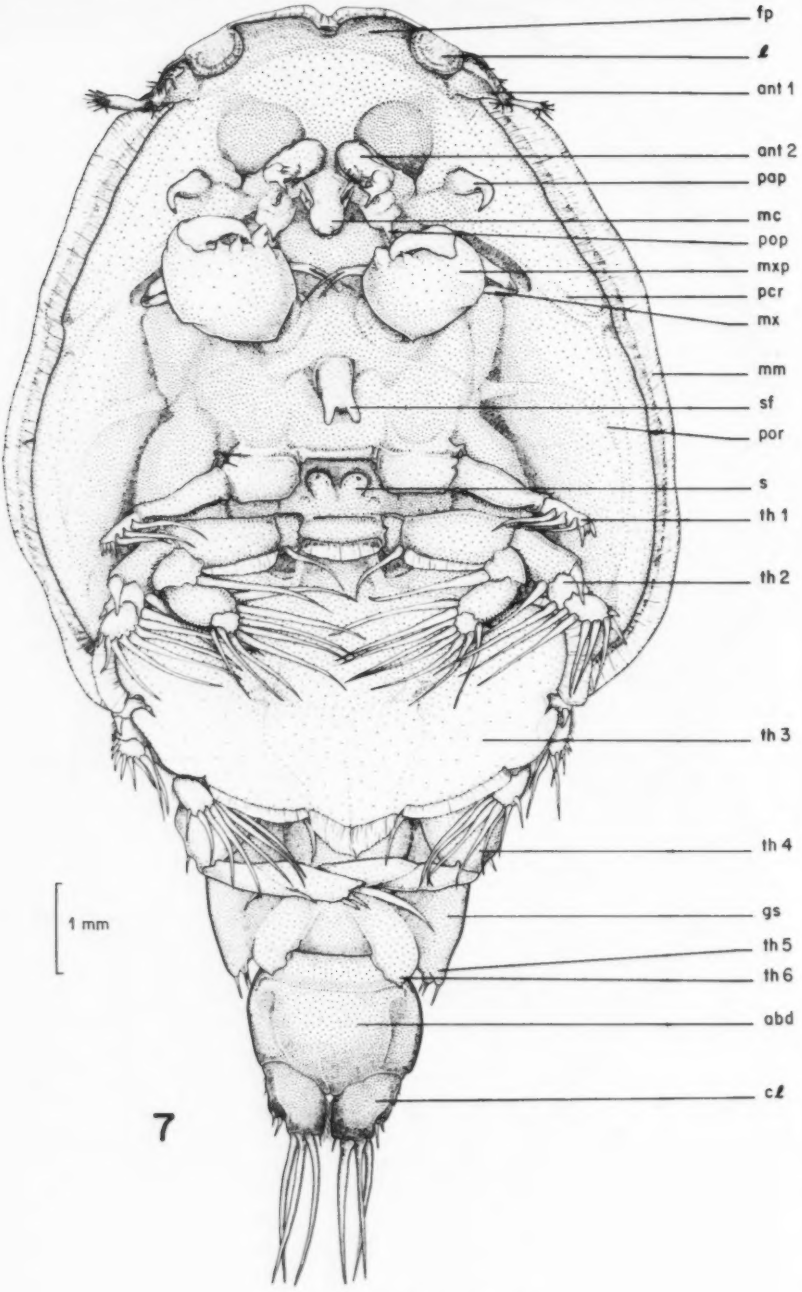


FIG. 7. Male, entire, ventral.

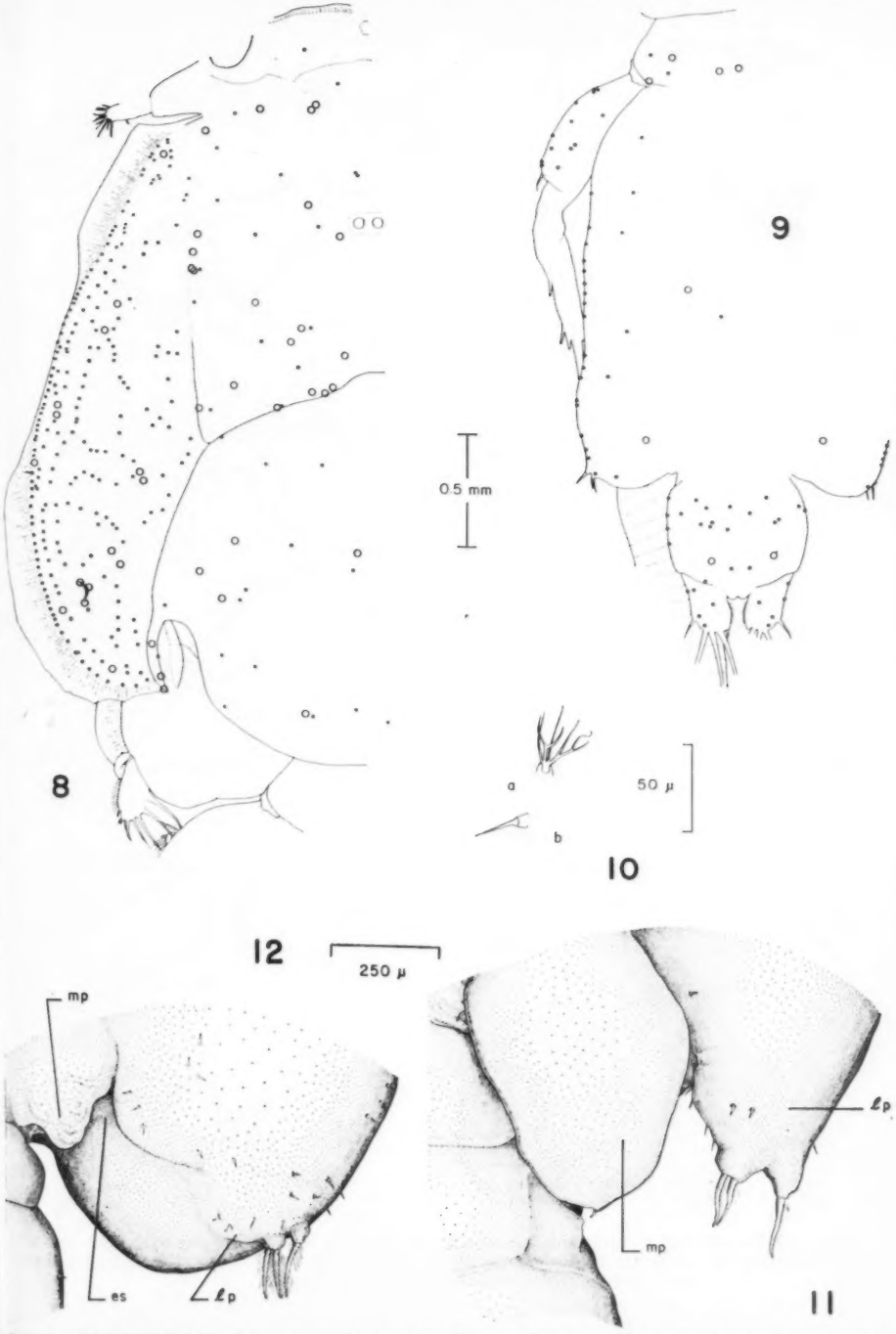


FIG. 8. Dorsal left half of carapace, showing distribution of sensory setae (see text). FIG. 9. Part of genital segment and entire abdomen, dorsal, showing distribution of sensory setae (see text). FIG. 10. Two types of sensory setae. FIG. 11. Posterolateral corner of male genital segment, ventral. FIG. 12. Posterolateral corner of female genital segment, ventral.

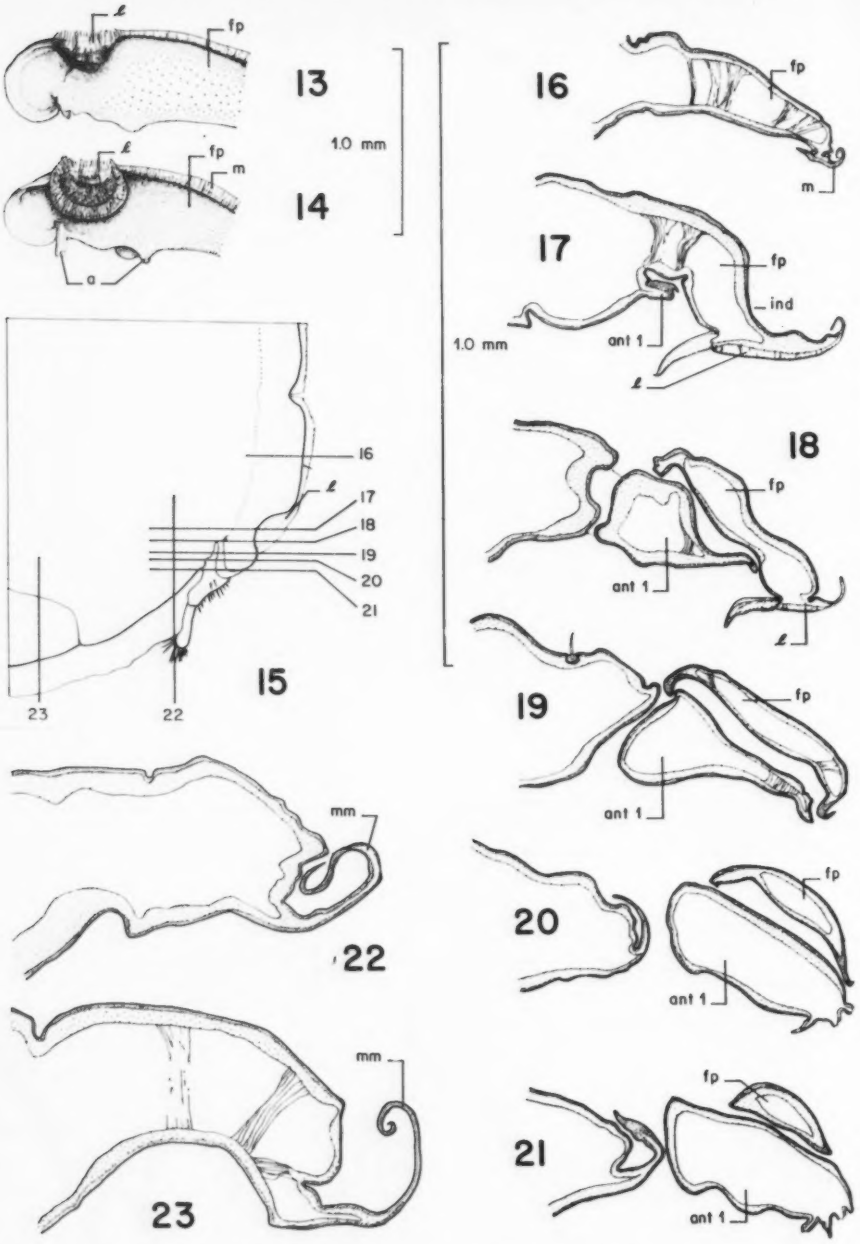
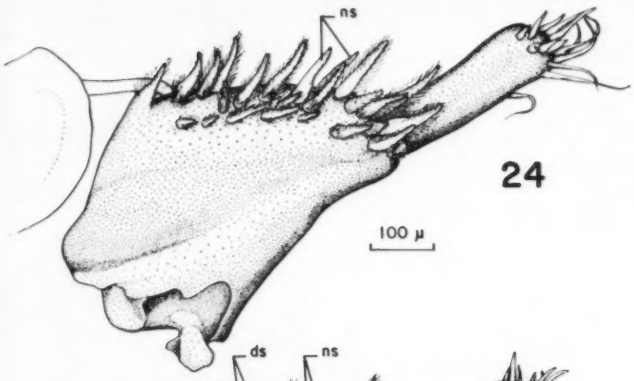
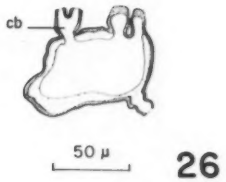
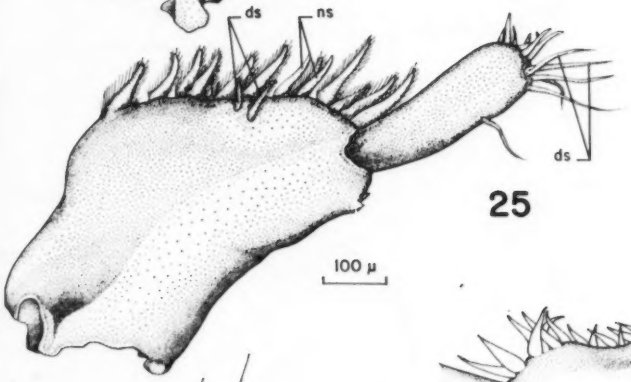
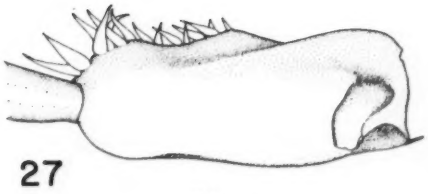


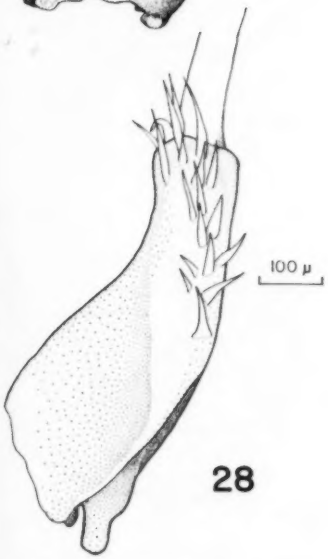
FIG. 13. Part of frontal plate and lunule, dorsal. FIG. 14. Same, ventral. FIG. 15. Anterolateral corner of carapace showing planes of sections. FIG. 16–23. Sections (drawn to same scale) through planes shown in Fig. 15.











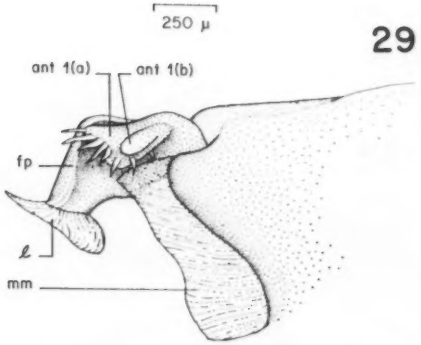


FIG. 24. 1st antenna, entire, ventral. FIG. 25. Same, dorsal. FIG. 26. 1st antenna, transverse section through tip. FIG. 27. 1st antenna, proximal, segment, posterior. FIG. 28. Same anterior. FIG. 29. Anterior margin of carapace and 1st antenna, lateral.

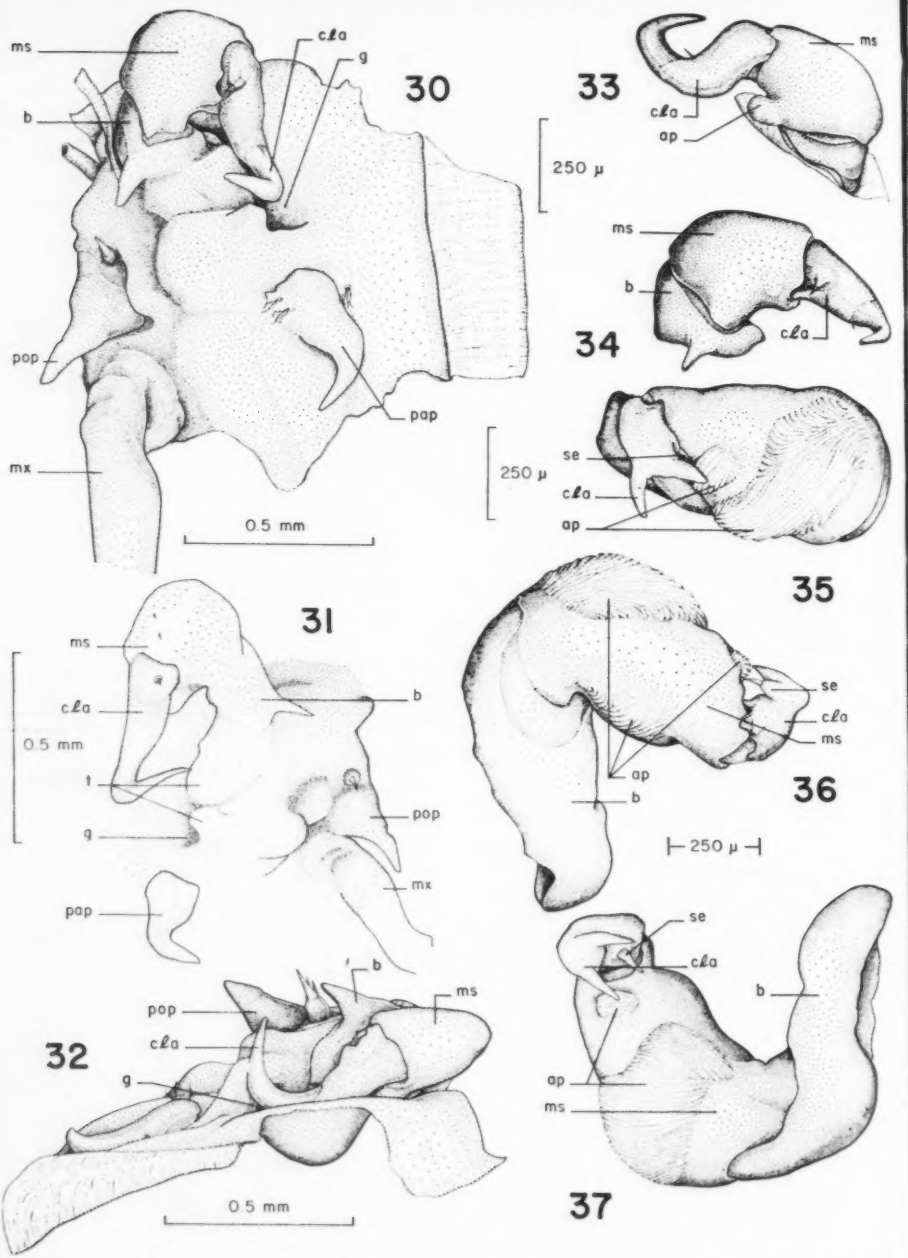


FIG. 30. Female 2nd antenna, half raised, ventral. FIG. 31. Same, erect. FIG. 32. Same, lowered, lateral. FIG. 33. Same, dorsomedial. FIG. 34. Same, posterior. FIG. 35. Male first antenna, ventral. FIG. 36. Same, anterior. FIG. 37. Same, posterior.

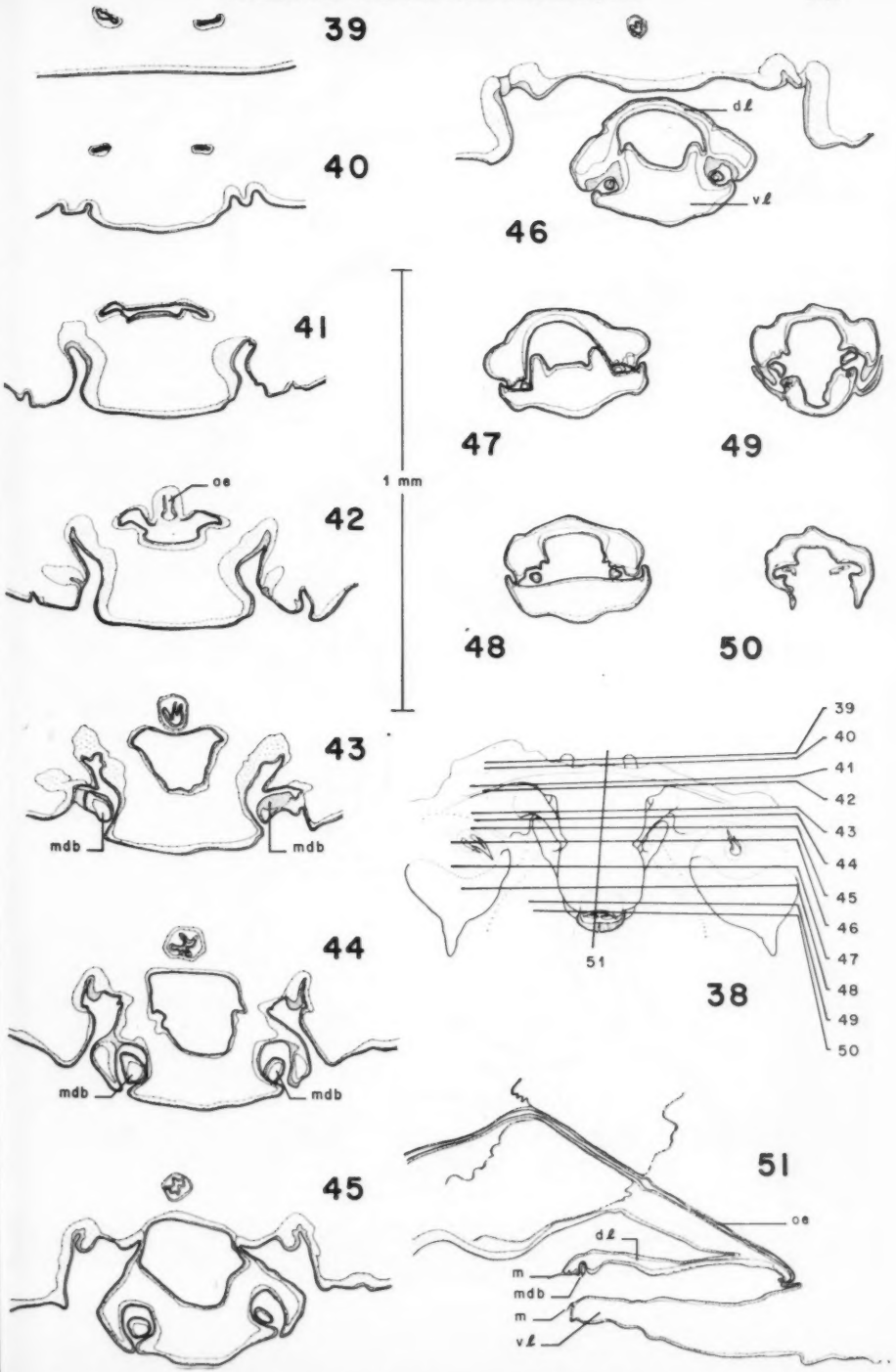


FIG. 38. Mouth tube in situ, ventral, showing planes of sections. FIG. 39–51. Sections (drawn to same scale) through planes shown in Fig. 38.

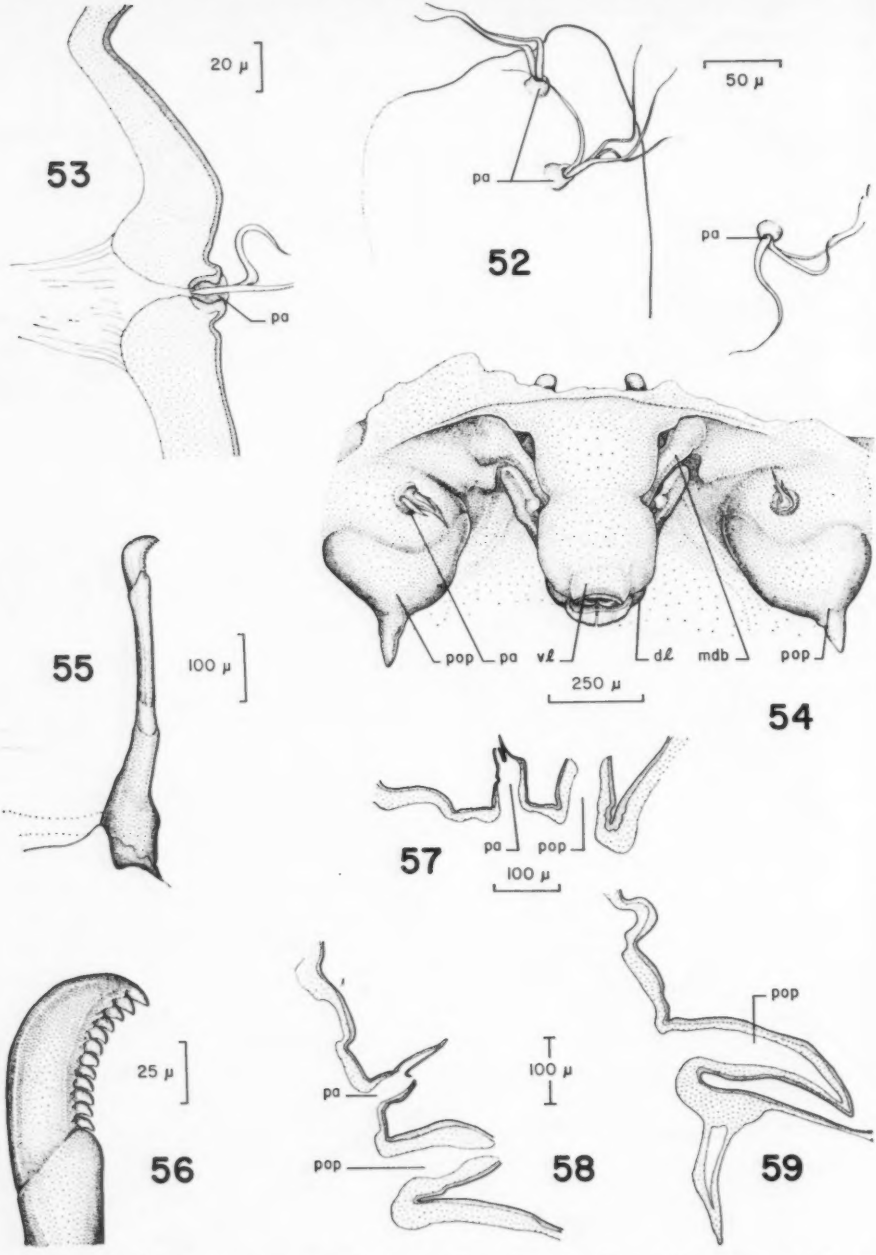


FIG. 52. Base of postantennal process, showing papillae. FIG. 53. Section through one papilla. FIG. 54. Mouth tube in situ. FIG. 55. Mandible, entire, lateral. FIG. 56. Same, tip. FIG. 57–59. Longitudinal sections through postoral process.

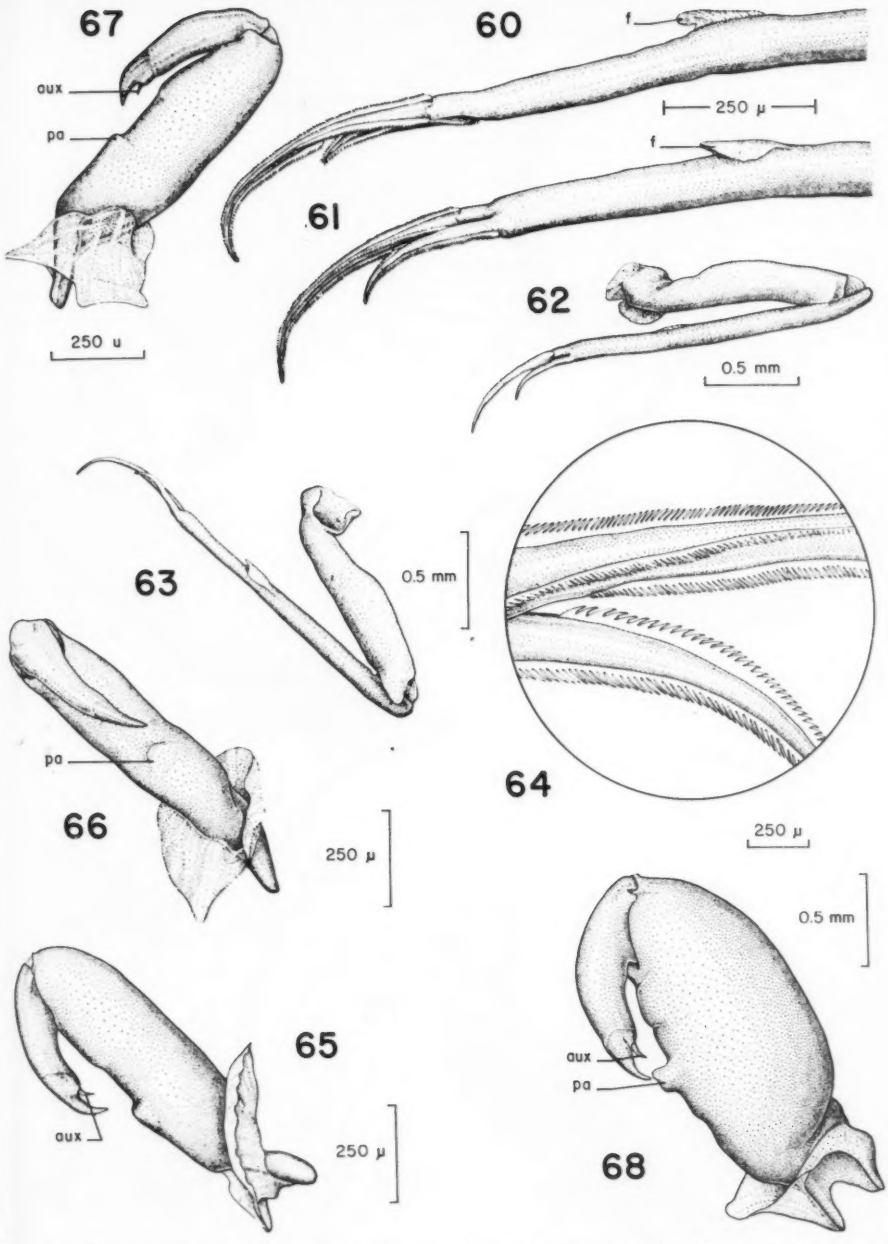


FIG. 60. Distal half of maxilla, ventral. FIG. 61. Same, dorsal. FIG. 62. Maxilla, entire, ventral. FIG. 63. Same, dorsal. FIG. 64. Detail of the terminal extensions of maxilla. FIG. 65. Maxilliped, female, dorsal. FIG. 66. Same, anterior. FIG. 67. Same, ventral. FIG. 68. Maxilliped, juvenile male, ventral.

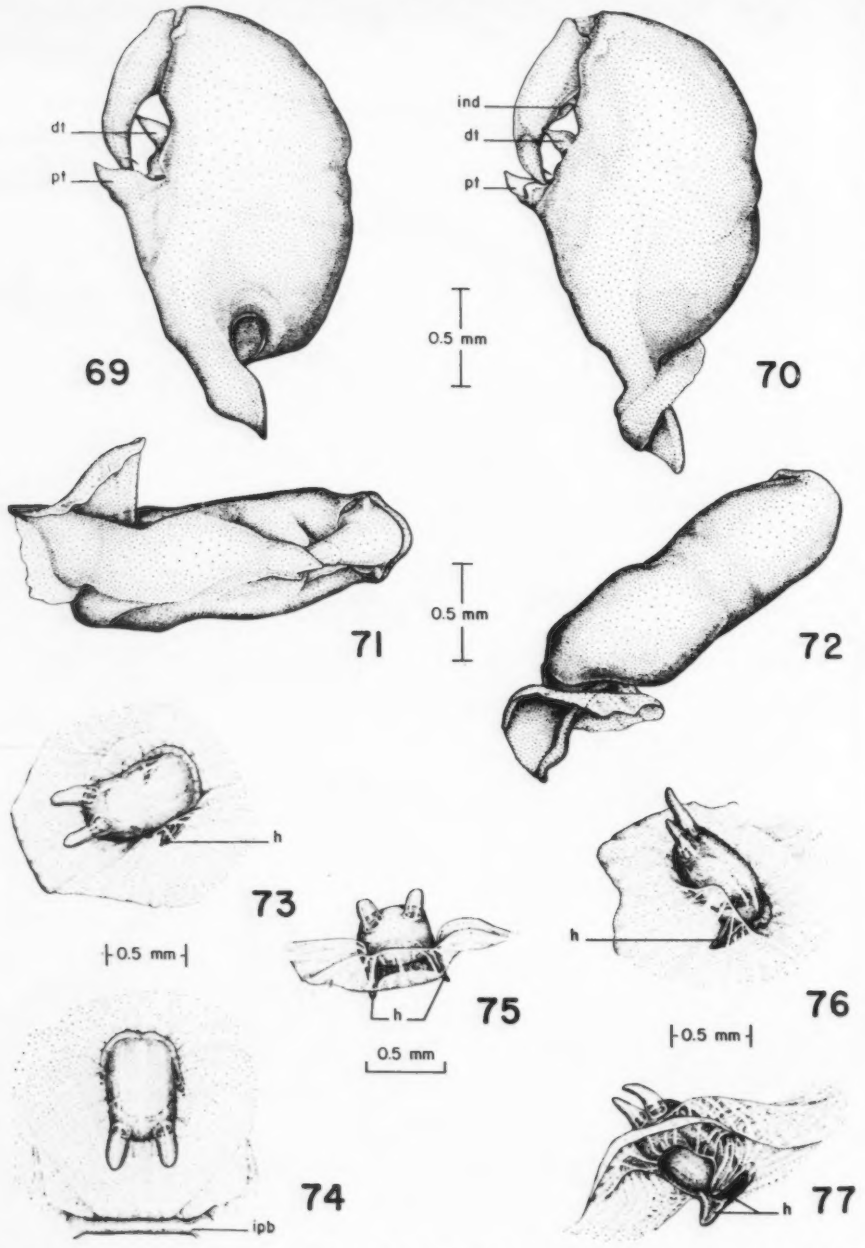


FIG. 69. Maxilliped, male, entire, dorsal. FIG. 70. Same, ventral. FIG. 71. Same, medial. FIG. 72. Same, lateral. FIG. 73. Sternal furca, ventrolateral. FIG. 74. Same, ventral. FIG. 75. Same, posterior. FIG. 76. Same, lateral. FIG. 77. Same, dorsolateral.

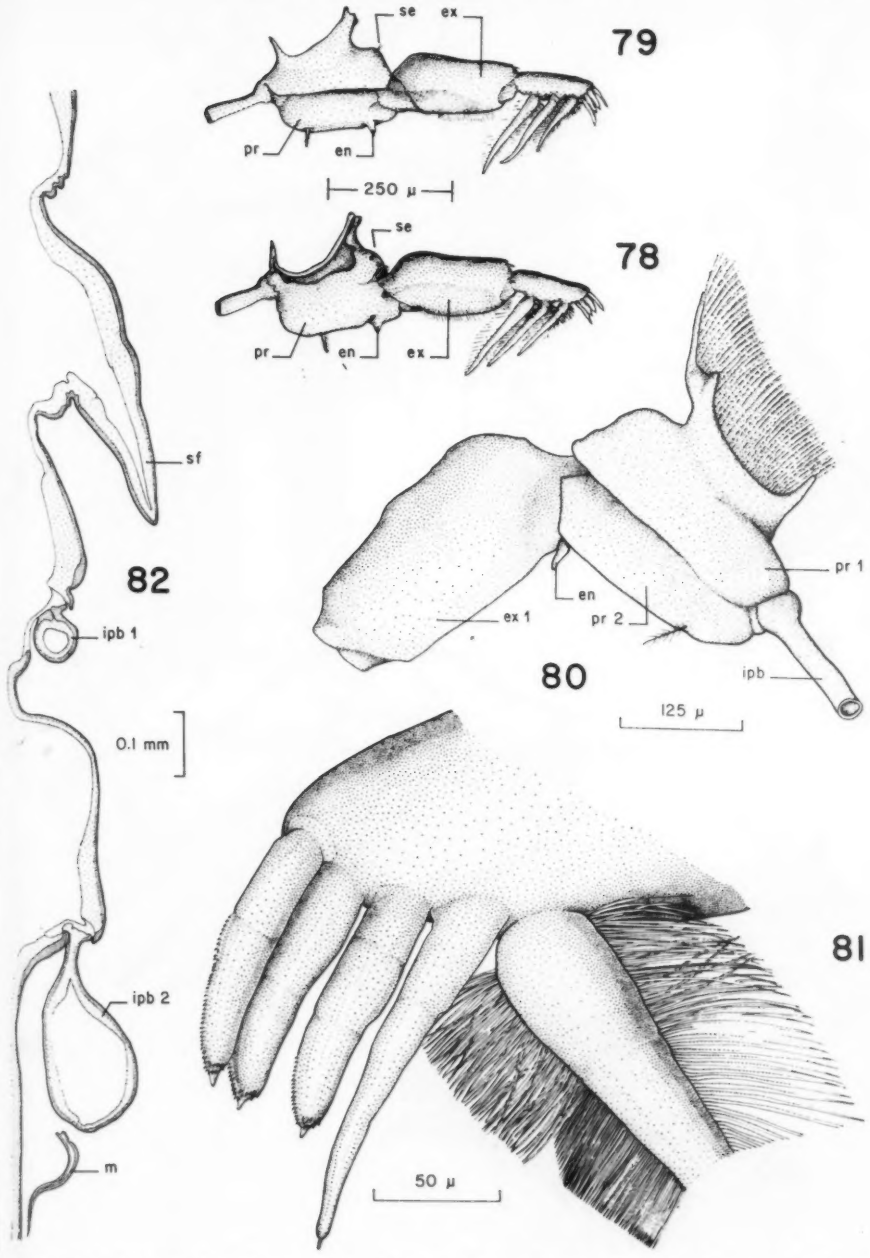


FIG. 78. 1st thoracopod, entire, ventral. FIG. 79. Same, dorsal. FIG. 80. Same, proximal part, posterior. FIG. 81. Same, tip of exopod, ventral. FIG. 82. Sagittal section in midventral line, part of ventral surface showing sternal furca, 1st and 2nd interpodal bars.

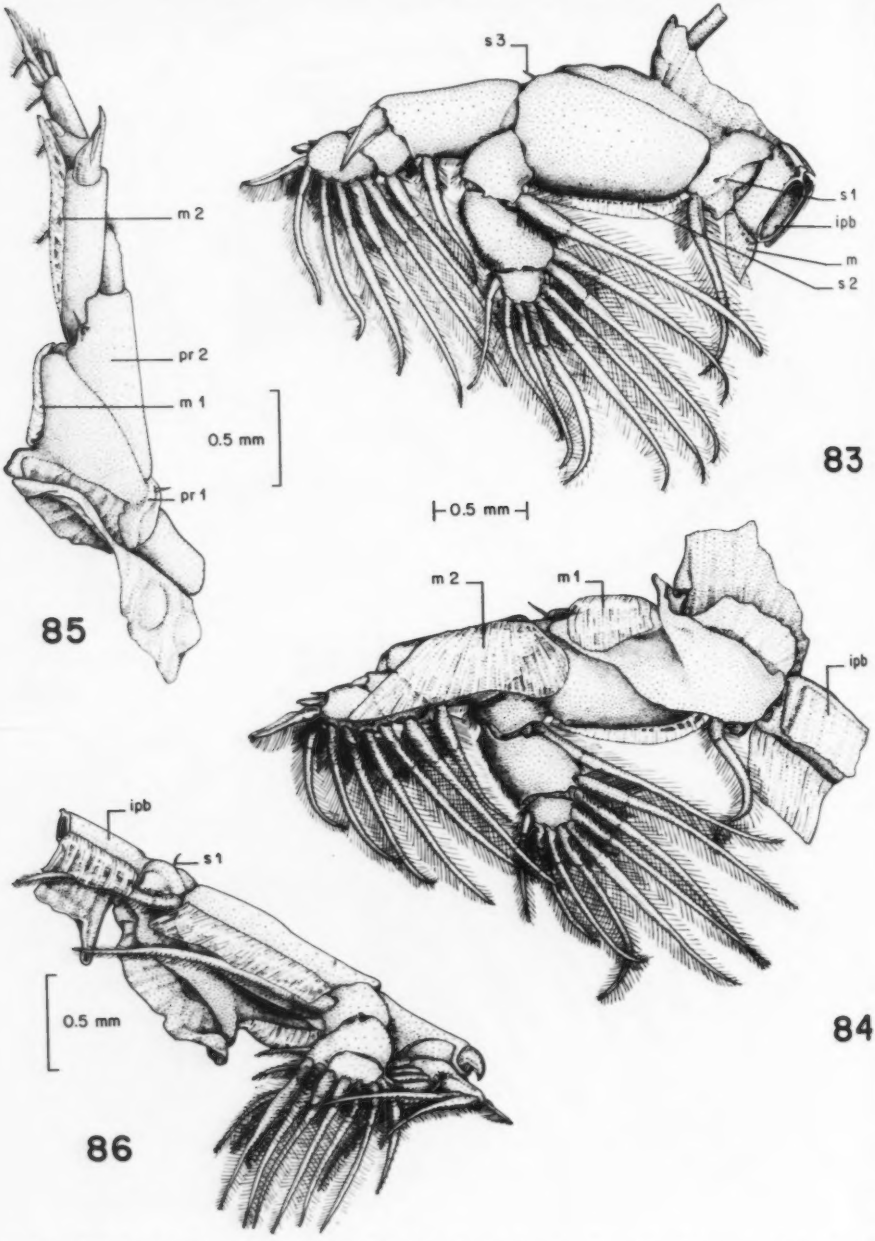


FIG. 83. 2nd thoracopod, entire, ventral. FIG. 84. Same, dorsal. FIG. 85. Same, anterior. FIG. 86. Same, posterior.

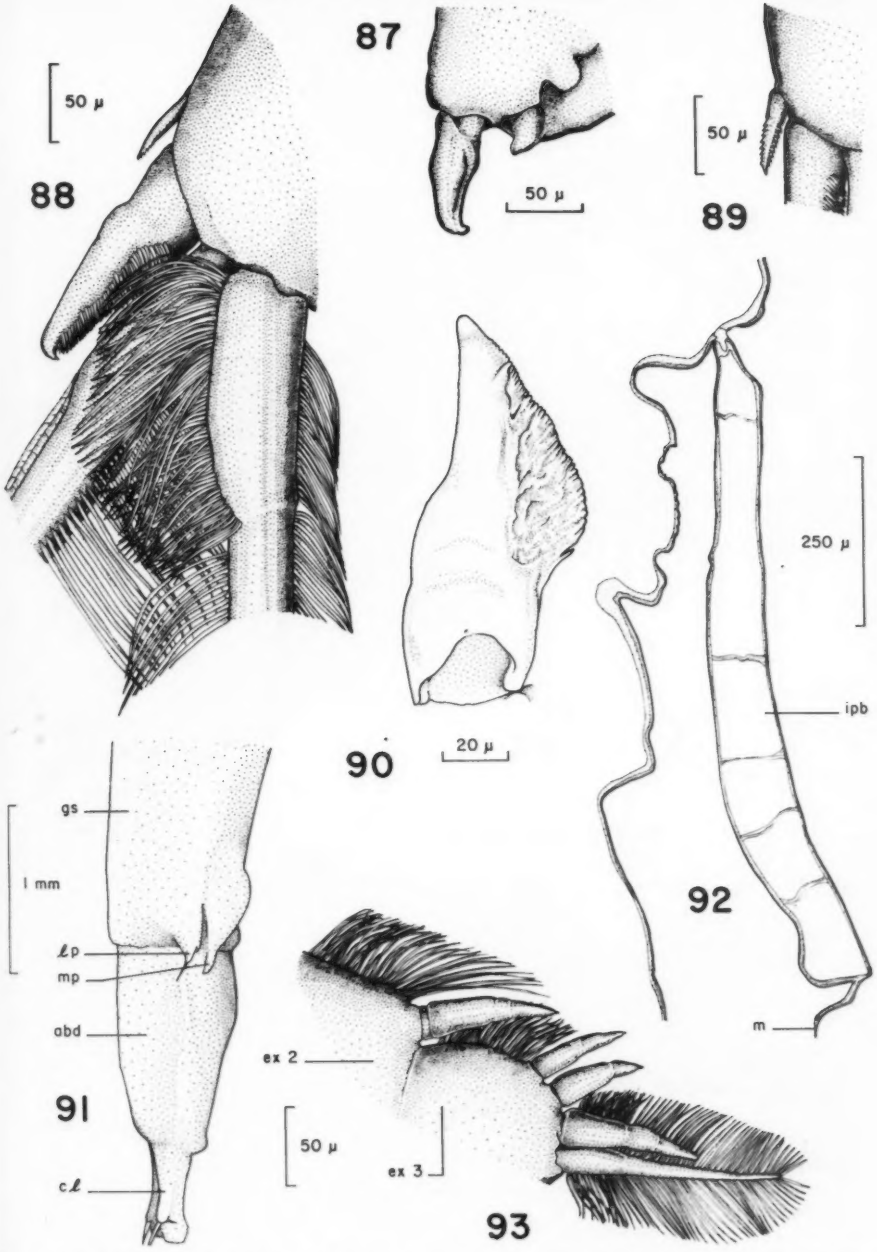
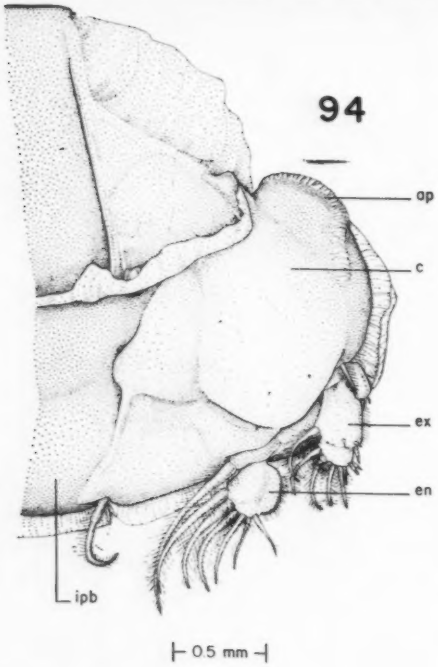
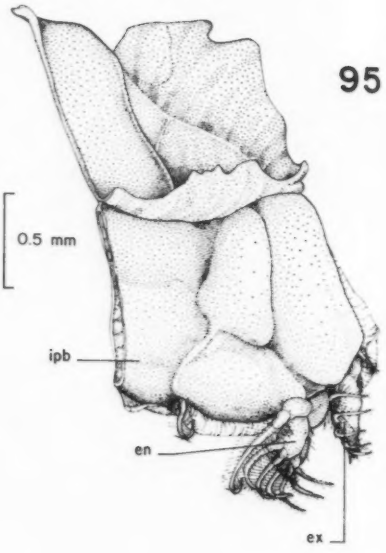


FIG. 87. 2nd thoracopod, details of marginal armature, 2nd exopodal segment. FIG. 88. Same, 3rd exopodal segment. FIG. 89. Spine of the 3rd exopodal segment. FIG. 90. Larger spine of 3rd exopodal segment, posterior. FIG. 91. Male, posterior part of genital segment and abdomen, lateral. FIG. 92. Sagittal section, interpodal bar of 3rd thoracopod. FIG. 93. 3rd thoracopod, details of exopodal armature.





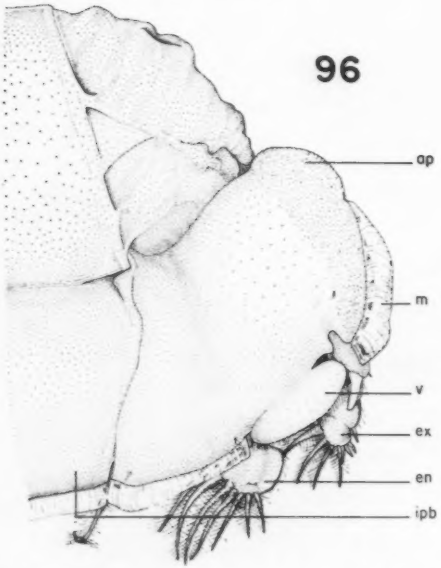


FIG. 94. 3rd thoracopod, entire, dorsal. FIG. 95. Same, dorsomedial. FIG. 96. Same, ventral.

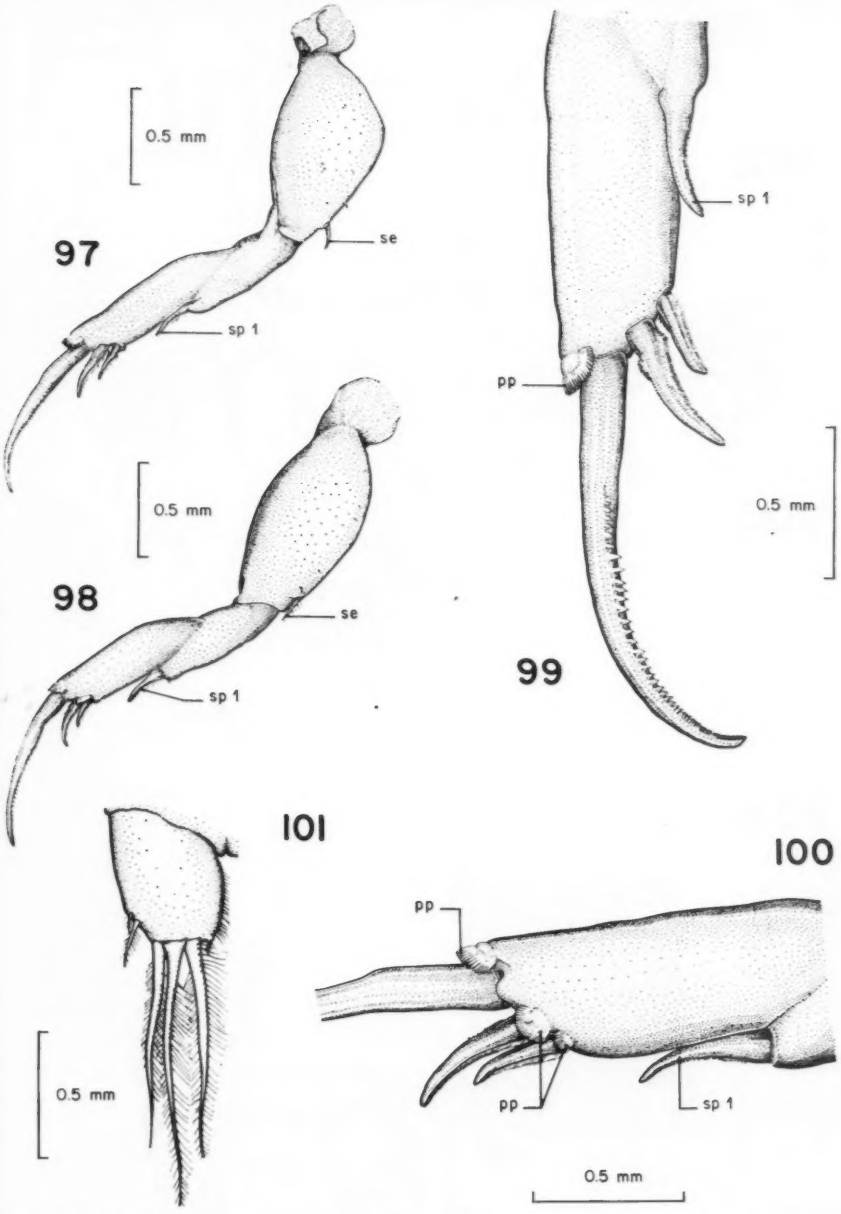
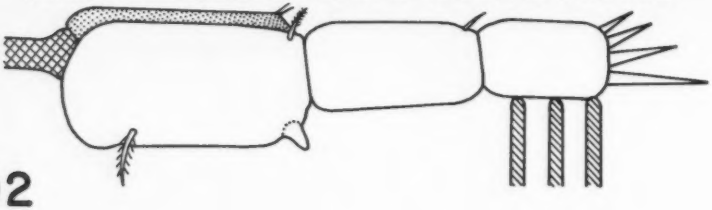
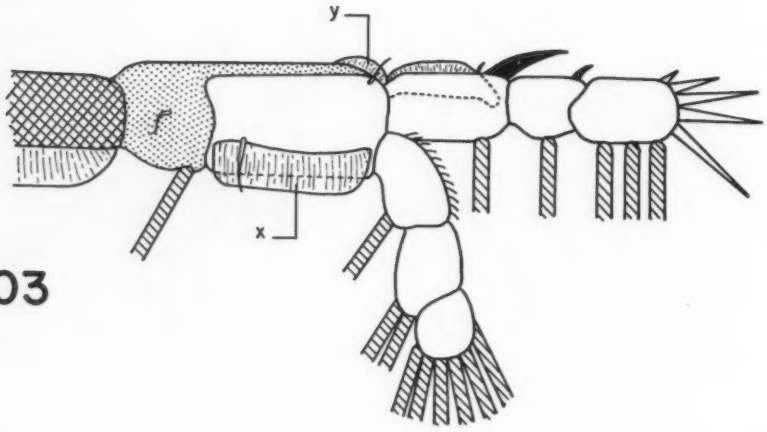


FIG. 97. 4th thoracopod, entire, dorsal. FIG. 98. Same, entire, ventral. FIG. 99. Same, tip, dorsal. FIG. 100. Same, tip, ventral. FIG. 101. Caudal lamella, ventral.



102



103

104

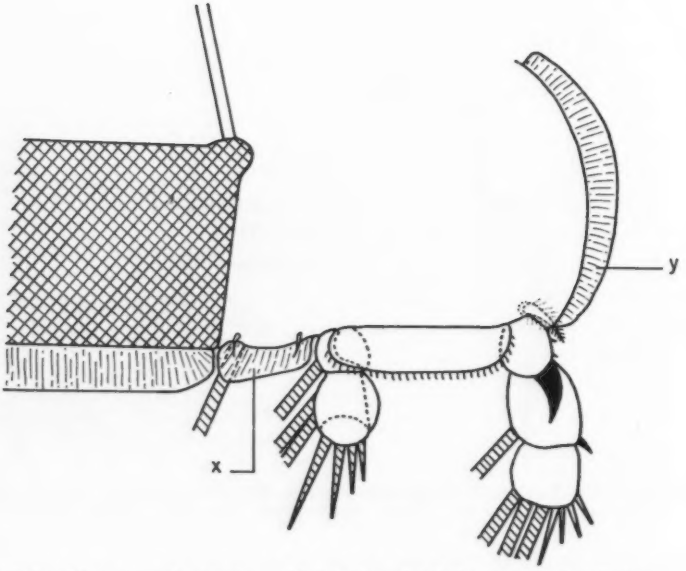
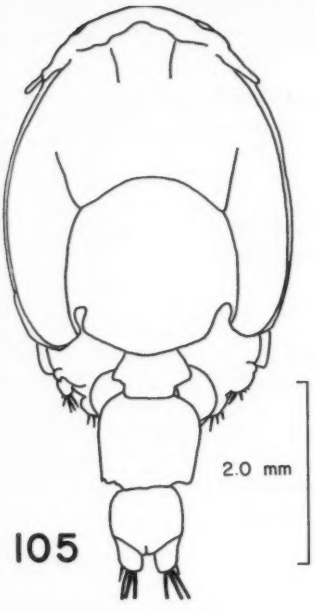
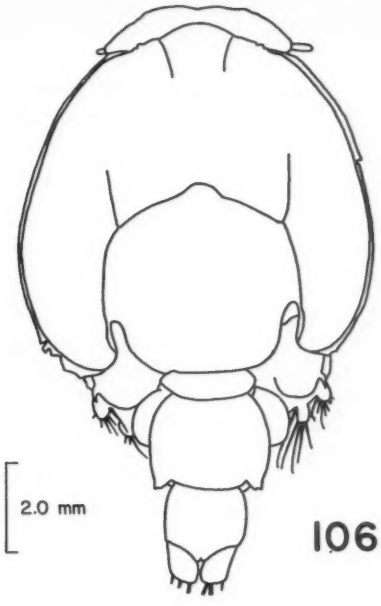
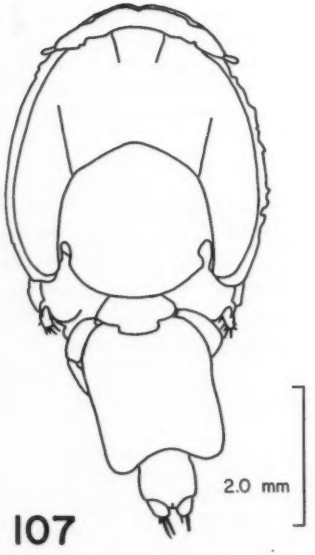


FIG. 102–104. Diagrammatic structure of 1st, 2nd, and 3rd thoracopods (see text).







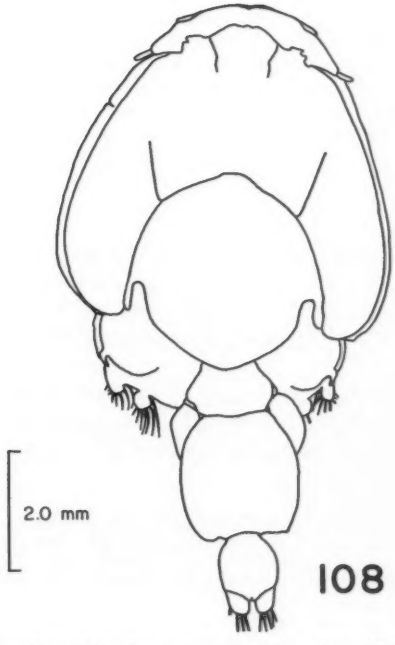


FIG. 105. Outline drawing, dorsal, of young male. FIG. 106. Same, mature male. FIG. 107. Same, gravid female. FIG. 108. Same, postgravid female.

Tests on the Accuracy of Ageing Chinook Salmon (*Oncorhynchus tshawytscha*) from their Scales[1]

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ABSTRACT

The accuracy with which several readers determined the ages of adult chinook salmon from their scales averaged 75% in a test that used scales from fish of known ages. Their consistency in assigning the same age to a scale when presented with the same selection of scales on two occasions averaged 76%. In these tests the readers derived age composition arrays which were similar to the true age compositions of the two samples. When several pairs of readers assigned ages to a large numbers of scales from fish of unknown ages agreement within pairs was good (roughly 75%), and among the pairs the derived age compositions were very similar. The levels of both accuracy and consistency achieved in these tests indicate that experienced personnel, using good scale-reading equipment, are able to produce age composition data that could be used as reliable parameters in chinook salmon population analyses.

INTRODUCTION

Salmon scale "readers" appear to be in general agreement that chinook salmon scales are particularly difficult to age with confidence. The difficulty arises from the complexity of the chinook salmon's life history, and because the life history of the species can vary considerably among stocks and races, and even among individuals of the same race.[2]

Young chinook salmon may migrate from fresh water to the ocean within hours of emergence, or after periods of residence that can vary from days, weeks, or months to as much as several years. They may remain at sea for

[1]Received for publication February 19, 1968.

[2]In this context a "stock" of salmon has the general meaning that they belong to a particular river system, including its tributaries (for example, the Fraser River stocks of chinook salmon, which are composed of a number of races). Using Mason's (1965) definition, a "race" is considered to be "a population of chinook salmon which spawns in a particular river or tributary at a particular time of the year."

J. Fish. Res. Bd. Canada, 25(9): 1971–1982, 1968.
Printed in Canada.

several months to as long as 6 or more years. Some young leave the stream at the very beginning of scale formation, whereas others migrate with the body fully covered with scales, and with scales that already show numbers of freshwater circuli.

Differences among young fish also occur, depending upon where and for how long they sojourn before they finally enter the ocean proper. Apparently there is much variation in the time they spend in or near river mouths or in estuaries. The wide range of physical and biological differences in both their freshwater and marine habitats is reflected in comparable variation in their growth and, in turn, therefore, in their scale patterns. To the scale reader the end result of all this variability in the life history of the chinook salmon, particularly during the early period, is that its scales are difficult to interpret for age because he frequently lacks the criteria upon which such an interpretation can be based with confidence.

In the current program to evaluate the efficiencies of chinook salmon hatcheries on the Columbia River,[3] the age compositions of the catches and escapements of chinook salmon are needed in computing the contributions of the hatcheries to the fisheries, and in computing the survival of different broods at different ages. Therefore, because it was recognized that there was a problem in the ageing of chinook salmon from their scales, tests were conducted to determine how well or how poorly chinook salmon scales could be read. The purpose of this document is to report the results of these tests.

METHODS

Three tests were made, each involving experienced scale readers from one Canadian and several United States fisheries agencies. In this report the scale readers and the agencies to which they belong are not identified; instead a letter serves to designate each individual reader.

In the first test 200 scales of known age were used. The ages were known because the scales came from recaptured hatchery fish that had been marked by a double finclip when liberated. Sets of impressions were made of these scales and sent to the different readers. No information, other than that they were chinook salmon scales, was provided to the readers. In some cases the readers were not aware that they were engaged in a test, or that the true ages of the scales they were examining were known. Those who selected the scales were not otherwise involved in the test. In addition, the selectors chose for the test only scales which they themselves considered readable.

Several months later impressions of these same scales, arranged in different order, were again sent to the readers. All other conditions of this second part of this test were the same as for the first. Thus, in the first test it was possible to determine each reader's accuracy in assigning an age to a scale,

[3]The main objective of this program is the assessment of the efficiency of several hatcheries in their production of autumn ("fall") runs of chinook salmon. This is being done by determining the catches (both sport and commercial from California to southeast Alaska) and escapements resulting from the releases of the progeny from four brood stocks (1961–64).

and also the consistency with which he assigned a particular age to each scale in the two readings.

In the second test the same 200 scales plus 200 similarly selected scales of known age were sent to the readers. However, on this occasion, for each of the 400 scales the fork length of the recaptured fish, and the month and location of its capture were provided. The main objective of this second test was to assess to what extent, if any, the readers were able to improve their age determinations by making use of the additional information. All other conditions of this test were the same as for the first.

In the third test scales of unknown age, taken from troll catches off the west coast of Vancouver Island, were used. The main objective of this test was to compare the age determinations made by different pairs of readers. As is commonly known, the west coast of Vancouver Island troll fishery exploits a mixture of stocks from many river systems and from United States hatcheries.

The equipment used by the different readers varied among the agencies (Appendix), but it was that which they preferred and with which they were most familiar.

The complete data produced by these tests are on file at the Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C.

RESULTS

Test 1. Scales of Fish of Known Age
scales 1–200, read twice

With each of the four readers, and in both readings of the first 200 scales, the errors in assigned ages included several age-classes and were sometimes high relative to the correct number of scales belonging to a particular age-class (Table I). However, among the 1600 determinations the total number of wrong age assignments was only 403, or 25.2%. In the first reading the correct assignments by the four readers averaged 76.0, 64.0, 69.5, and 83.0% of the 200 scales, and in the second reading, 82.5, 60.0, 77.0, and 86.5% (Table II). For the four readers and the two readings combined, the overall average was 74.8% correctly assigned.

The rates of consistency with which the four readers assigned a particular age (correctly or incorrectly) to each scale in the second reading were 79.5, 69.0, 72.0, and 83.5% (Table III). The average for the four readers amounted to 76.0% — that is, among them they gave the same age assignments to 608 out of 800 determinations at the second reading as they had done at the first. All four readers achieved a high rate of consistency with scales which they considered to be of age 0.2 (range, 76.1–95.6%).

As might be expected, the readers' consistency in general paralleled their accuracy. The two more important exceptions to this were with scales which were read (correctly or incorrectly) as 0.1's and 0.2's. As the following tabulation indicates, which is based on all the readings, the readers tended

TABLE I. The ages assigned to the first 200 scales, by four readers for each of the two readings separately and for both readings combined, as percentages of the number of scales of each true age-class.[a]

True age	No. of scales	First reading										Second reading									1st and 2nd readings combined									
		0.1	0.2	1.1	0.3	1.2	0.4	1.3	2.2	1.0	NR[b]	0.1	0.2	1.1	0.3	1.2	0.4	1.3	2.2	NR	0.1	0.2	1.1	0.3	1.2	0.4	1.3	2.2	1.0	NR
Reader A																														
0.1	31	45.2	41.9	6.5							6.5	64.5	29.0	6.5							54.8	35.5	6.5							3.2
0.2	115		80.9		12.2	6.1					0.9		89.6		3.5	6.1				0.9		85.2		7.8	6.1					0.9
1.1	2		50.0	50.0									50.0	50.0								50.0	50.0							
0.3	38				86.8	2.6		2.6			7.9		5.3		89.5					5.3		2.6		88.2	1.3		1.3			6.6
1.2	10				20.0	70.0					10.0		10.0		30.0	50.0				10.0		5.0		25.0	60.0					10.0
1.3	4							100.0								50.0		50.0							25.0		75.0			
Reader B																														
0.1	31	74.2	25.8									54.8	35.5	3.2		3.2	3.2				64.5	30.6	1.6		1.6	1.6				
0.2	115	3.5	65.2		28.7	1.7		0.9					64.3	0.9	31.3	1.7	1.7				1.7	64.8	0.4	30.0	1.7	0.9	0.4			
1.1	2		50.0	50.0										50.0	50.0							50.0	50.0							
0.3	38		7.9	2.6	55.3	31.6	2.6						5.3		50.0	36.8	2.6		5.3			6.6	1.3	52.6	34.2	2.6		2.6		
1.2	10		10.0		30.0	50.0		10.0							40.0	50.0	10.0					5.0		35.0	50.0	5.0	5.0			
1.3	4					25.0		75.0										100.0							12.5		87.5			
Reader C																														
0.1	31	74.2	6.5	12.9						6.5		80.6	6.5	12.9							77.4	6.5	12.9							3.2
0.2	115	2.6	80.9		12.2	4.3						2.6	80.0	0.9	14.8	1.7					2.6	80.4	0.4	13.5	3.0					
1.1	2			50.0	50.0									50.0	50.0								50.0	50.0						
0.3	38		28.9	5.3	39.5	15.8	2.6	2.6	5.3				10.5	2.6	73.7	13.2						19.7	3.9	56.6	14.5	1.3	1.3	2.6		
1.2	10		10.0		20.0	50.0		20.0					30.0		20.0	40.0			10.0			20.0		20.0	45.0		10.0		5.0	
1.3	4					50.0		50.0										100.0							25.0		75.0			
Reader D																														
0.1	31	61.3	22.6	12.9	3.2							61.3	29.0	9.7							61.3	25.8	11.3	1.6						
0.2	115	1.7	89.6		7.0	1.7							97.4		2.6						0.9	93.5		4.8	0.9					
1.1	2		50.0	50.0									50.0	50.0								50.0	50.0							
0.3	38		5.3		84.2	10.5							5.3	2.6	78.9	13.2						5.3	1.3	81.6	11.8					
1.2	10		10.0	10.0	10.2	70.0							20.0		10.0	70.0						15.0	5.0	10.0	70.0					
1.3	4							100.0										100.0									100.0			

[a]In this report ages are designated according to the European system. Thus, a 0.1 fish has no freshwater annulus, but has one ocean annulus; it is therefore in its 2nd year of life, having gone to sea in its 1st. A 1.2 fish has one freshwater annulus and two ocean annuli; it is therefore in its 4th year of life, having gone to sea in its 2nd. According to the Gilbert and Rich (1927) system, the fish in these two examples would have had ages designated as 2_1 and 4_2 respectively.

[b]Not read.

to be more consistent in reading scales as 0.1's and 0.2's than they were accurate in assigning ages to 0.1 and 0.2 scales:

True age:	0.1	0.2	1.1	0.3	1.2	1.3
No. of readings	248	920	16	304	80	32
% accuracy	62.2	81.1	50.0	69.2	58.6	82.1
% consistency	72.8	87.1	55.6	63.8	61.0	61.1

TABLE II. Percentages of correct assignments for each age-class in two readings of first 200 scales by four readers.

True age	No. of scales	Reader A	A	B	B	C	C	D	D	Avg
0.1	31	45.2	64.5	74.2	54.8	74.2	80.6	61.3	61.3	64.5
0.2	115	80.9	89.6	65.2	64.3	80.9	80.0	89.6	97.4	81.0
1.1	2	50.0	50.0	50.0	50.0	50.0	50.0	50.0	50.0	50.0
0.3	38	86.8	89.5	55.3	50.0	39.5	73.7	84.2	78.9	69.7
1.2	10	70.0	50.0	50.0	50.0	50.0	40.0	70.0	70.0	56.3
1.3	4	100.0	50.0	75.0	100.0	50.0	100.0	100.0	100.0	84.4
Total or avg	200	76.0	82.5	64.0	60.0	69.5	77.0	83.0	86.5	74.8

TABLE III. The consistency with which the four readers assigned the same age to a scale in the second reading of the first 200 scales as they did in the first.[a]

Ages assigned	Consistency No.	%	Ages assigned	Consistency No.	%
	Reader A			***Reader B***	
0.1	13/15	86.7	0.1	17/27	63.0
0.2	98/109	89.9	0.2	67/88	76.1
1.1	3/3	100.0	1.1	1/2	50.0
0.3	34/51	66.7	0.3	37/57	64.9
1.2	9/7	52.9	1.2	12/20	60.0
1.3	2/5	40.0	0.4	1/1	100.0
Total	159/200	79.5	0.3	3/5	60.0
			Total	138/200	69.0
	Reader C			***Reader D***	
0.1	22/28	78.6	0.1	15/22	68.2
0.2	85/101	84.2	0.2	108/113	95.6
1.1	4/7	57.1	1.1	2/6	33.3
0.3	24/48	50.0	0.3	30/42	71.4
1.2	7/11	63.6	1.2	8/13	61.5
1.3	2/4	50.0	1.3	4/4	100.0
NR	0/1	0.0	Total	167/200	83.5
Total	144/200	72.0			

[a]Whether or not a reader made a correct or an incorrect age assignment at either reading is, of course, ignored in this comparison.

[b]Not read.

Among the 403 instances of misageing, 44 (10.9%) were due to under-ageing by 1 ocean year, but with the correct freshwater age; 200 (49.6%) were due to over-ageing by 1 or more ocean years, but with the correct freshwater age; and 107 (26.6%) were due to assigning 1 freshwater year to scales that had none (however, of these, 51, or 12.7% of the 403 misaged scales, had been given the correct total age). Of the remaining 52 (12.9%) scales, 12 (3.0%) were not assigned ages; 23 (5.7%) had the correct total age, but both the freshwater and ocean ages wrong; and 17 (4.2%) had other errors. Of the 1588 scales that were read, 1271 (80.0%) had been given the correct total age; 1381 (87.0%) had been given the correct freshwater age; and 1255 (79.0%) had been given the correct ocean age.

Test 2. Scales of Fish of Known Age

Scales 1–400, read with information on capture of fish

In general, little improvement resulted from readers being supplied with information for each scale on the fork length of the fish, and the month and place of its capture (Table IV). The principal exception to this was with the

Table IV. The percentages of correct age assignments which readers achieved in tests 1 and 2.[a]

Reader	1	2	3	4	1	2	3	4	1	2	3	4
	Age 0.1				*Age 0.2*				*Age 1.1*			
A	45.2	64.5	67.7	82.0	80.9	89.6	87.0	68.0	50.0	50.0	50.0	–
B	74.2	54.8	90.3	92.0	65.2	64.3	69.6	68.0	50.0	50.0	50.0	–
C	74.2	80.6	83.9	90.0	80.9	80.0	93.0	68.0	50.0	50.0	50.0	–
D1	61.3	61.3	83.9	94.0	89.6	97.4	87.8	68.0	50.0	50.0	50.0	–
D2	–	–	83.9	92.0	–	–	97.4	88.0	–	–	50.0	–
	Age 0.3				*Age 1.2*				*Age 0.4*			
A	86.8	89.5	94.7	70.0	70.0	50.0	40.0	–	–	–	–	62.0
B	55.3	50.0	89.5	78.0	50.0	50.0	60.0	–	–	–	–	76.0
C	39.5	73.7	73.7	48.0	50.0	40.0	40.0	–	–	–	–	40.0
D1	84.2	78.9	86.8	82.0	70.0	70.0	60.0	–	–	–	–	88.0
D2	–	–	92.1	90.0	–	–	30.0	–	–	–	–	86.0
	Age 1.3				*All ages*							
A	100.0	50.0	75.0	–	76.0	82.5	82.5	70.5				
B	75.0	100.0	100.0	–	64.0	60.0	76.5	78.5				
C	50.0	100.0	100.0	–	69.5	77.0	85.0	61.5				
D1	100.0	100.0	100.0	–	83.0	86.5	85.5	83.0				
D2	–	–	–	–	–	–	90.5	89.0				

[a]Column 1 — first reading of first 200 scales, read with no accompanying information; column 2 — second reading of first 200 scales, read with no accompanying information; column 3 — third reading of first 200 scales, read with information on fork length and month and place of capture; column 4 — only reading of second 200 scales, read with information on fork length and month and place of capture. (Readers D1 and D2 were attached to the same fisheries agency.)

0.1 fish. With this age-class the third reading of the first 200 scales, and the single reading of the second 200 scales, provided rates of correct age assignment by all readers that were appreciably higher than those achieved when the scales were read without the additional information.

True and Assigned Age Compositions

The two tests provided 18 separate age composition arrays which can be compared with the true age compositions of the two samples. Regardless of the errors that they made (as has been described in the foregoing text), most of the readers derived age compositions which were fairly similar to the true ones (Table V). The most prominent exception to this was with the single reading of the second lot of 200 scales (despite the fact that these scales were accompanied with information on length and time and place of capture), when the five readers together named six age-classes which were not actually present in the sample.

Three factors were probably mainly responsible for the degree of accuracy which the readers attained in determining the age compositions of the two samples: (*a*) in most instances the readers correctly interpreted in terms of freshwater and ocean ages what they identified on the scales as circuli and annuli; (*b*) all the readers had some general knowledge of the life history of chinook salmon, and specifically of the ages at which they commonly spawn or are taken in the fisheries, and this knowledge no doubt influenced to some degree their interpretations of the markings on the scales which they observed; (*c*) in each test the readers made errors of both over-ageing and under-ageing, which, by offsetting each other, promoted a more correct derivation of the *age composition* than would have been the case had their errors been in one direction only.

Test 3. Scales of Fish of Unknown Age

The main objective of this test was to compare the age assignments made by all of the readers by pairs. Five of the readers attempted to age all of the 928 scales, one reader examined 500 scales, and the seventh examined 300.

With scales which both of a pair of readers aged, the overall rate of agreement between the two readers averaged 76.6%, and ranged from 66.6 to 86.9% among the 20 different pairs (Table VI). Also, *on the average*, the pairs of readers considered 25.4% of the scales to be not readable, the range between pairs being 9.3–28.1%. The *average* number of scales which one of a pair aged but not the other amounted to only 5.4% (range, 3.2–12.0%).

All the readers found seven different age-classes, and no more, among the scales which they were able to age (Table VII).

The accuracy of the readers' age assignments cannot, of course, be assessed, since the true ages of these fish were not known. However, agreement among readers, which would indicate the level of confidence that might be attached to their results, can be examined by comparing the age compositions

TABLE V. The age compositions (percentages) derived by each reader compared with the true age compositions.[a]

Reader	Age 0.1	0.2	1.1	0.3	1.2	1.3	1.0	0.4	2.2
First reading of first 200 scales read without additional information									
A	7.3	55.4	1.6	25.4	7.8	2.6	–	–	–
B	13.5	44.0	1.0	28.5	10.0	2.5	–	0.5	–
C	13.0	53.5	3.5	16.0	9.0	2.5	1.0	0.5	1.0
D	10.5	57.0	3.0	21.0	6.5	2.0	–	–	–
True age	15.5	57.5	1.0	19.0	5.0	2.0	–	–	–
Second reading of first 200 scales read without additional information									
A	10.2	59.2	1.5	20.9	1.7	1.0	–	–	–
B	8.5	43.5	1.5	30.0	11.0	2.0	–	2.5	1.0
C	14.1	50.8	3.5	24.1	5.5	2.0	–	–	–
D	9.5	63.0	2.5	17.0	6.0	2.0	–	–	–
True age	15.5	57.5	1.0	19.0	5.0	2.0	–	–	–
Third reading of first 200 scales read with information on fork length, month, and place of capture									
A	10.8	57.2	1.5	22.7	6.2	1.5	–	–	–
B	14.0	41.0	1.0	35.0	6.0	3.0	–	–	–
C	13.0	56.0	2.5	16.5	7.0	3.5	0.5	–	1.0
D1	13.0	53.5	1.5	24.5	5.0	2.0	–	0.5	–
D2	13.5	61.5	1.0	20.5	1.5	2.0	–	–	–
True age	15.5	57.5	1.0	19.0	5.0	2.0	–	–	–

Single reading of second 200 scales read with information on fork length, month, and place of capture

	Age 0.1	0.2	0.3	0.4	1.1	1.2	2.1	1.3	0.5	1.4
A	24.4	20.9	26.2	19.2	–	4.1	–	2.9	0.6	1.7
B	23.5	18.0	29.0	20.5	1.0	–	–	3.0	–	5.0
C	23.1	18.1	18.1	12.6	1.5	2.5	1.0	8.5	0.5	14.1
D1	24.0	19.0	27.5	23.5	0.5	1.5	–	2.5	–	1.5
D2	24.2	24.7	26.3	22.2	0.5	–	–	0.5	–	1.5
True age	25.0	25.0	25.0	25.0	–	–	–	–	–	–

[a]In computing a reader's age composition any scales which he did not read were not included.

TABLE VI. Comparisons between pairs of readers who read chinook salmon scales of unknown age from the west coast of Vancouver Island. Five readers read all 928 scales; a sixth, 500; and a seventh, 300.

Pair	Scales aged by both readers Agreement (%)	Scales not aged by either reader (%)	Scales not aged by one reader (%)
	All (928) scales		
1×2	78.6	28.1	4.0
1×3	82.4	27.8	5.0
1×4	66.7	27.2	4.8
1×5	74.6	26.5	5.5
2×3	81.1	26.5	5.2
2×4	75.4	26.7	4.2
2×5	74.1	26.2	4.7
3×4	74.1	26.7	4.2
3×5	79.8	25.4	5.6
4×5	66.6	25.9	3.9
	500 scales		
1×6	79.6	25.0	7.4
2×6	78.4	25.8	4.6
3×6	84.5	24.0	7.6
4×6	73.1	24.8	4.6
5×6	80.8	25.8	3.2
	300 scales		
1×7	80.3	20.3	12.0
2×7	79.5	9.3	9.3
3×7	84.3	19.3	8.3
4×7	68.5	19.7	7.3
5×7	86.9	19.0	10.0
Total or avg	76.6	25.4	5.4

derived by the various pairs, using only those scales to which each member of a pair gave the same ages (both fresh water and ocean). This has been done in Table VII for the five readers who attempted to read all of the 928 scales.

In terms of the derived age compositions of the sample the agreement between the 10 pairs of readers was very good. The greatest difference among the 10 pairs of readers was with the 0.2 age-class — thus, pair 2 × 4 read 53.6% of the sample as 0.2 fish as compared with 64.8% by pair 2 × 5, a range of 11.2%. The smallest difference between the pairs was with the 0.1 age-class — thus, three pairs of readers read 3.2% of the sample as 0.1 fish as compared with 4.0% by pair 1 × 4 (a difference of 0.8%).

DISCUSSION

From the tests that made use of scales of known age it may be concluded that: (*a*) the degree of accuracy achieved in reading all the scales varied among the readers, but the overall average of approximately 75% can be considered

TABLE VII. The age compositions (percentages) derived by pairs of readers, using only those scales on whose ages they agreed. Test 3; 928 scales of unknown age.[a]

Readers	0.1	0.2	1.1	0.3	1.2	0.4	1.3
1×2	3.2	59.2	1.2	24.0	8.5	1.2	2.6
1×3	3.3	60.9	1.2	22.6	8.6	0.6	2.9
1×4	4.0	56.3	1.4	27.6	6.9	1.2	2.6
1×5	3.2	64.3	1.1	23.4	5.7	0.6	1.7
2×3	3.3	60.9	1.2	24.5	7.2	0.8	2.1
2×4	3.3	53.6	1.7	30.8	5.2	2.5	2.9
2×5	3.2	64.8	0.8	25.3	4.0	0.6	1.3
3×4	3.6	56.8	1.7	27.2	7.4	0.8	2.5
3×5	3.3	64.6	0.8	24.5	5.1	0.6	1.2
4×5	3.7	60.1	1.4	28.8	4.4	0.7	0.9
Range	0.8	11.2	0.9	8.2	4.6	1.9	2.0

[a]Each pair of readers agreed upon approximately 75% of the scales which they examined.

adequate; (*b*) the degree of accuracy differed with the true age-class, and scales with both freshwater and ocean annuli were misaged more frequently than those with only saltwater annuli; (*c*) information on length of fish and time and place of capture was of some value in improving the interpretation of the 0.1 fish, but was not especially beneficial otherwise; there is no reason to think that such information would be particularly useful in determining the ages of fish in samples comprising mixed stocks and races (except, possibly, in the case of the 0.1 fish, whose small size would likely prompt caution in assigning older ages); (*d*) the degree of consistency in reading these scales was relatively high, averaging 76% among four readers; (*e*) the age compositions of the two samples derived by the several readers were very similar, and approximated the true age compositions. To some extent this resulted from balancing-out over-ageing by under-ageing, but it was mainly due to the accuracy with which readers assigned ages to scales.

In the test which used the large number of scales from fish of unknown age, taken from catches of mixed populations, the levels of agreement within pairs of readers in assigning ages to scales were high. Also, the age composition arrays derived from these scales by 10 pairs of readers were very similar.

Thus, it is the writers' opinion that experienced salmon scale readers, using good equipment, can derive chinook salmon age composition data that are sufficiently accurate as to make them useful parameters for salmon population analyses.

A further point might be discussed. Does the accuracy achieved in assigning ages to chinook salmon scales differ significantly from that achieved with the scales of other Pacific salmon? At this time we have only certain sockeye salmon data that might be compared. Actual *accuracy* cannot be compared because the true ages of these fish were not known. However, Table VIII

TABLE VIII. The percentage agreement achieved by pairs of readers who aged sockeye salmon scales of Canadian (100 scales), Japanese (100 scales), and United States (255 scales) origin.[a]

Pairs of readers:	AB	AC	AD	AE	AF	BC	BD	BE	BF
Canadian sockeye	90.0	91.0	91.0	92.0	–	83.0	82.0	88.0	–
Japanese sockeye	45.0	76.0	75.0	75.0	67.0	46.0	47.0	46.0	44.0
U.S. sockeye	65.5	76.5	78.4	71.4	70.6	58.0	56.5	53.7	50.2
Pairs of readers:	CD	CE	CF	DE	DF	EF			
Canadian sockeye	100.0	85.0	–	86.0	–	–			
Japanese sockeye	87.0	83.0	75.0	85.0	81.0	78.0			
U.S. sockeye	82.4	78.0	77.7	75.7	75.3	87.1			

[a]Data from Anon. (1956). The Japanese sockeye were taken on the high seas, so that their actual origin is not known; it could have been either Asian or North American, or both.

shows the *degree of agreement* reached between pairs of readers who determined the ages of sockeye salmon scales obtained from Japanese, United States, and Canadian sources (Anon., MS, 1956).[4] The comparison makes it very apparent that there were many cases of disagreement. (The scales included freshwater ages of from 1 to 4 years, and total ages of from 2 to 7 years; the consistent high rate of agreement achieved with the Canadian scales was no doubt due to the fact that among them there were fewer age-classes (both ocean and freshwater) than there were among the Japanese and United States scales.)

In this report no material is presented that describes the different kinds of scales used in the tests, nor is an attempt made to indicate the specific characteristics of scales upon whose interpretation the readers either agreed or disagreed. Probably, there will always be considerable disagreement in the interpretation of individual chinook salmon scales, even among experienced scale readers. The reasons for this, as has been mentioned, arise from the complexity and variability in the life history of the chinook salmon. However, the results of the tests do suggest that improvement in accuracy and/or consistency might be achieved in several ways. In the first place, it is considered that to attain high levels of *consistency* in assigning ages, good, modern equipment must be used (see Appendix), and the readers should be trained and experienced. Secondly, the fund of reliable criteria that could be used in making interpretations of scale patterns must be increased, if improvements in either accuracy or consistency are to be made. This could be achieved if information gained from examining chinook salmon scales from many sources, of fish which have experienced a wide variety of environments, could be disseminated more widely. Finally, the results of the tests suggest that useful criteria for interpreting scales probably also would be gained if readers could compare

[4]See footnote to Table VIII.

the processes by which they gave age assignments to individual scales, particularly those scales on whose ages they disagreed.

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APPENDIX — EQUIPMENT USED

The following apparatus was used by the several agencies participating in these tests:

OREGON FISH COMMISSION (REGIONAL OFFICE, CORVALLIS)
Eberbach Projector, Cat. No. 72–402, with 24-inch screen and 80× magnification.

OREGON FISH COMMISSION (RESEARCH HEADQUARTERS, CLACKAMAS)
Bausch & Lomb Tri-Simplex micro-projector, vertical (downward) projection, 21–23× magnification (occasionally, 42–46× for more detailed study).

WASHINGTON STATE DEPARTMENT OF FISHERIES (OLYMPIA)
Monocular microscope mounted on a Spencer Ortho-Illuminator; Model 600; with prism and mirror for reflection to table. Magnification from 6 to 90×. Detailed description given by R. R. Mandapat, Washington Department of Fisheries, in "Age analysis technique, utilizing fish scales, presently used by the Washington Department of Fisheries." Manuscript, 1968.

UNITED STATES BUREAU OF COMMERCIAL FISHERIES, SEATTLE, WASHINGTON
Microscope with a 90° prism and plate glass mirror for projection onto white celluloid sheet. Magnifications of 40 and 82.5× used. Detailed description given by K. H. Mosher in U.S. Fish and Wildlife Service Bull. No. 54, Vol. 51, 1950.

FISHERIES RESEARCH BOARD OF CANADA (BIOLOGICAL STATION, NANAIMO, B.C.)
Leitz Prado No. 500 micro-projector, Cat. No. 34010A; vertical projection by means of ocular prism and mirror; 100× magnification.

NOTES

Suggested Physiological Interaction among Rainbow Trout Fingerlings Undergoing Thermal Stress

Allee et al. (1963) have pointed out that "a biologically conditioned medium such as water in which fish have lived may produce beneficial results on later inhabitants."

While determining the resistance of rainbow trout fingerlings to high lethal temperatures, I obtained preliminary data suggesting that fish withstand heat stress longer in water previously "conditioned" by the former presence of other fish than in water which is initially fresh. Fingerlings weighing approximately 2 g were obtained from a private hatchery (Spring Valley Trout Farm, Waterloo County, Ontario) and acclimated to 15 C in the Aquarium Room of the University of Waterloo, in running, aerated well water. During the acclimation period they were fed fish pellets (Glencoe Mills, Minnesota) and were in apparent good health. The water used in the tests was conditioned by raising it to a lethal temperature and exposing samples of trout to this warm water until heat death occurred. Conditioned and "fresh" water were drawn from the same reservoir to insure that both samples had the same initial level of air saturation. The lethal test baths consisting of 5-liter plastic pails, were filled with water and maintained at a constant temperature (±0.1 C). Aeration and stirring were simultaneously provided by compressed air introduced by an air breaker. Oxygen concentration and *p*H did not vary significantly throughout an experiment.

Heat resistance was expressed as the time to heat narcosis — a stage in the progress towards thermal death at which a fish, although near death and almost motionless, recovers if rescued and returned to the acclimation bath. In the present study it was arbitrarily assumed to occur 15 sec after the frequency of opercular movements fell below a rate of one every 30 sec. Fish when removed at this point usually recovered within several minutes.

Three series of experiments were carried out. In the first, samples of four trout were netted at random from the holding bath and divided into two sets of two fish. The first pair were placed in a lethal test bath at 29.0 C and the times to heat narcosis for each fish determined. At the completion of this test the fish were removed and the times to heat narcosis for the second pair noted in the same water and recorded. This procedure was repeated for other samples of four and heat resistances of corresponding pairs compared statistically. Similar tests were carried out at 28.5 C.

In the second experiment samples of five fish were used and divided into control and experimental groups. The water in which the experimental groups were tested was conditioned by previously subjecting eight fish to heat death

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at a lethal temperature. Control groups were tested simultaneously at the same temperature in water drawn from the reservoir.

In the third experiment two samples of 15 fish were tested by a different procedure. Resistance times of the control group were determined by testing each fish one after the other with water in the bath changed between successive determinations. Each fish of the control group was thus tested in water uncontaminated by the presence of other fish. The fish of the experimental group were also tested individually in the same manner but the water of the test bath was not changed throughout the course of the 15 determinations. Thus only the first fish of the experimental group was tested in fresh water. Each of the remaining 14 individuals was tested in water conditioned by the fish preceding it.

Tables I, II, and III contain the resistance times of individual fish in control and experimental groups. It has been shown by Fry et al. (1946) and

TABLE I. Time (minutes) to the onset of heat narcosis in rainbow trout fingerlings in fresh and conditioned water.

Trial:	1	2	3	4	5	6	7	8
			Test temp 29.0 C					
Fresh water	0.6	1.3	1.2	1.7	2.3	2.3	2.5	10.3
	0.8	2.8	1.3	1.8	4.7	21.0	2.5	17.5
Conditioned water	0.7	2.1	1.3	1.7	2.0	13.1	3.0	9.5
	2.3	3.2	1.8	5.2	3.8	13.0	11.2	9.4
			Test temp 28.5 C					
Fresh water	1.5	1.5	2.2	2.3	2.5	3.9		
	3.5	6.8	9.5	3.3	6.4	3.6		
Conditioned water	18.5	2.6	2.0	3.1	6.3	3.8		
	20.3	7.2	4.3	18.3	9.1	3.4		

TABLE II. Time (minutes) to the onset of heat narcosis in four samples of rainbow trout tested at 27.0 C in fresh and conditioned water.

Sample	Conditioned water		Sample	Fresh water	
1	1	52	3	1	50
	2	62		2	52.5
	3	63		3	52.5
	4	77		4	58.5
	5	90		5	59
2	1	50	4	1	40
	2	55		2	48
	3	70		3	50
	4	85		4	55
	5	125		5	65

TABLE III. Time (minutes) to the onset of heat narcosis of rainbow trout at 28.0 C in fresh and conditioned water (see text for details of testing).

Fresh water					
1. 2.9[a]	*4.* .66	*7.* 5.1	*10.* 2.0	*13.* 1.6
2. 2.5	*5.* 1.1	*8.* 2.2	*11.* 2.8	*14.* 3.0
3. 2.8	*6.* 3.0	*9.* 3.1	*12.* 4.0	*15.* 2.7
Conditioned water				
1. 1.5	*4.* 3.1	*7.* 3.9	*10.* 5.3	*13.* 6.0
2. 3.1	*5.* 2.1	*8.* 2.1	*11.* 4.8	*14.* 6.6
3. 3.2	*6.* 3.5	*9.* 4.0	*12.* 12.3	*15.* 5.0

[a]Arranged in order of testing.

later confirmed by many subsequent studies that the logarithms of the resistance times of fish undergoing heat death are normally distributed about a mean. The data of the first two experiments and the control group of the third experiment when plotted on semilog probit paper conform to this general rule. The logarithms of the resistance times of fish tested in conditioned water in the third experiment, however, were found to be assymmetrically distributed. The normal distribution of the data of the first two experiments permitted the application of the *t*-test. A distribution-free method, however, had to be applied to the data of the third experiment.

No statistically significant difference was revealed between the two groups tested at 29.0 C by the paired *t*-test ($P = .01$) although an effect was evident between the groups tested 0.5 C degree lower. In the second experiment the mean resistance time of the group in conditioned water was significantly longer than the control group (simple *t*-test, $P \leq .05$).

Resistance times of the two groups of fish of the third experiment were compared by making the hypothesis that the median resistance time of the control group was a good estimate of the median of the general population and that the experimental group represented a random sample of 15 taken from this population. In the experimental group 12 of the 15 individual resistance times exceeded this median. Since the probability that the median would be exceeded this many times as calculated by the point binomial is less than 0.01, it is concluded that the experimental group display a significantly higher heat resistance than the control.

The data of the above experiments indicate that fish undergoing thermal stress may alter the composition of the surrounding water, such that survival times of fish subsequently subjected to lethal temperatures in the same water are measureably increased. Whatever the reasons for the observed increase in heat resistance may be, future investigation of this phenomenon requires the identification of substances present in the water during heat death and a study of their effects on fish.

The magnitude of the group effects revealed in the present experiments is small and likely plays an insignificant role in lethal temperature determinations. Test baths are large relative to the size of the fish and water exchange usually adequate to prevent any significant accumulation of excreted substances.

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Temperatures of Red and White Muscle in Recently Caught Marlin and Other Large Tropical Fish

Carey and Teal (1966) described temperature gradients in two species of tuna which retain body heat by a counter-current heat exchange system probably unique to the scombrid fishes. This note provides information on temperature gradients within the bodies of some large nonscombrid fish which do not attain the high temperatures of tuna but which are nevertheless appreciably warmer than the surrounding water.

Materials and methods.— Temperatures were measured with a battery-powered 6-channel thermistor thermometer (Fig. 1) having five ranges of 10 C

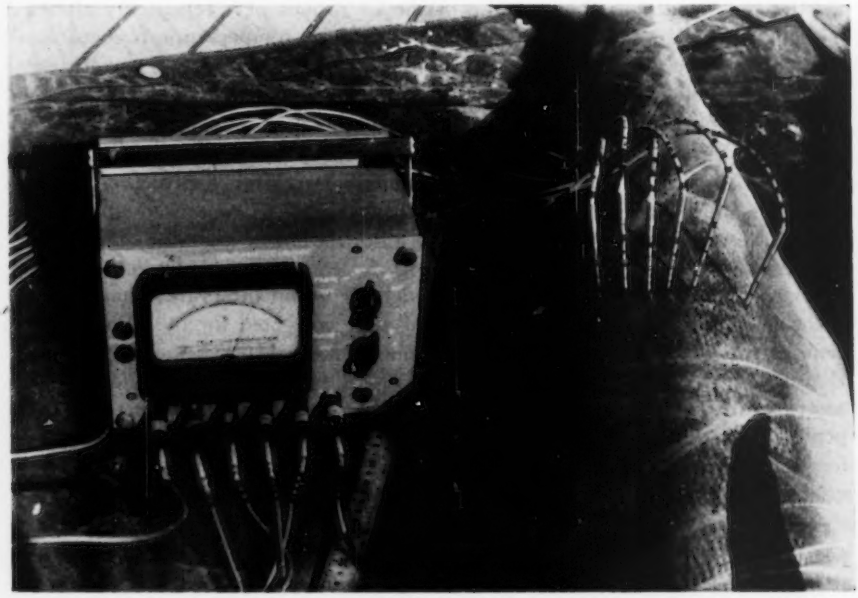

FIG. 1. Electric thermometer with probes inserted in left side of striped marlin (fork length 230 cm, weight 49 kg) opposite origin of anal fin. The wooden scale is marked in centimeters.

each and scale divisions of 0.2 degree C (Yellow Springs Instrument Co. Model 46TUC). The instrument was calibrated against a standard mercury thermometer. Thermistor probes were jacketed in stainless steel, 13 × 0.4 cm (Y. S. I. Model 403), marked at 1-cm intervals with bands of black vinyl ink, and had a response time of 1.6 sec. Observations were made on seven striped marlin, *Makaira mitsukurii* (fork lengths 205–243 cm); five dolphin,

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Coryphaena hippurus (77–98 cm); five Sierra mackerel, *Scomberomorus sierra* (45–63 cm); two Mexican barracuda, *Sphyraena ensis* (40.5–54 cm); and one black skipjack, *Euthynnus lineatus* (70 cm). Fish were caught between March 5 and 15, 1966, by trolling close to the surface within 15 miles either of Mazatlan or Cape San Lucas in Mexico at the southern end of the Gulf of California. Sea surface temperatures, measured in shade at a depth of 1.5 m, ranged from 20.6 to 22.9 C. Hooked fish were played on rod and line (for average times of 16 min for marlin and about 6 min for other species), lifted on deck with a gaff hook, and stunned or killed either by clubbing on the head or by severing the spinal cord behind the skull with a knife point. Except for the three dolphin referred to later, no fish showed subsequent movement other than a rare and brief muscular quiver. Fish were laid in the shade, and during most observations were repeatedly doused with buckets of sea water. Thermistor probes were inserted, and a series of temperatures was recorded while the depths and sometimes the positions of the six probes were repeatedly altered. Time which elapsed between landing and first temperature observations varied from 2 to 8 min, and was 5 min for the marlin in Fig. 2. Temperatures were monitored for at least 15 min, until gradients became established due to heating or cooling from the outside.

The number of probes, and time required for recording and moving them, restricted the amount of information available from each fish before internal gradients were lost; therefore, some fish were used to explore temperatures in an antero-posterior direction, some in a dorso-ventral direction, and others in a transverse plane. In constructing Fig. 2, temperatures were recorded for the whole sequence of points at least twice, at 9-min intervals. Changes due to heating or cooling during this interval were corrected for by adjusting all temperatures to a single intermediate time; almost all adjustments were less than 0.1 degree C, and none exceeded 0.15 degree C. Some error in absolute temperatures may have been introduced by the thermal capacity of the probes, but the general pattern of temperature indicated in Fig. 2 persisted for many minutes and was repeatedly registered despite changes in the sequence of probe movements.

Results.— In all fish, internal temperatures exceeded surface water temperature. Maximum recorded excess over water temperature for each species was: black skipjack, 10.2 C; striped marlin, 2.55 C; dolphin, 2.3 C; Mexican barracuda, 1.4 C; Sierra mackerel, 1.15 C. In three dolphins, which were evidently not killed outright when landed, temperature rises of as much as 1.0 degree C occurred over a 5-min period, during which time some muscular contractions were seen. In these three fish the temperature rise took place deep within the muscles and was not attributable to warming from the air. In all other fish the maximum internal temperature was probably highest early in the observations. The phenomenon of internal temperature rise subsequent to capture has been observed for other species, usually when the fish has remained alive and struggling.

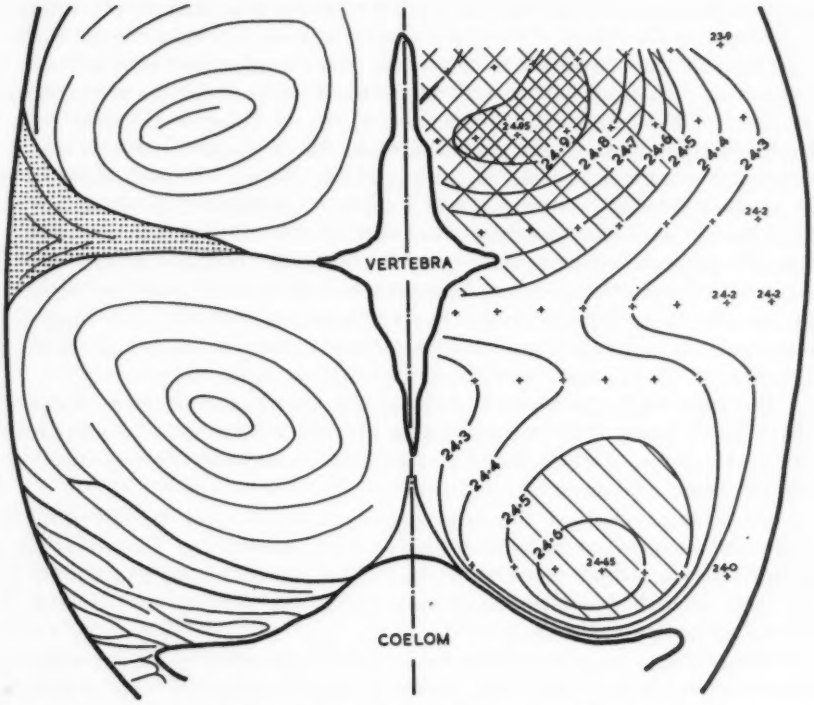

FIG. 2. Transverse section through marlin shown in Fig. 1 at level of probes (dorsal and ventral extremities of section omitted). Left side (mirror image of tracing from photo of sectioned fish) shows concentric hypaxial and epaxial white muscle blocks, with wedge of red muscle (stippled) between. Right side shows temperature isotherms (C), 13 min after fish clubbed, constructed from temperatures recorded at each of the probe positions marked by crosses (which were at 1-cm depth intervals). Fish played 14 min. Surface water 22.7 C.

In striped marlin the highest temperature was not in the centre of the body, but rather in or close to the centres of the epaxial muscle masses on either side of the mid-line (Fig. 2). Both at the level of the centre of the epaxial muscles, and also at a level slightly below the centre of the hypaxial muscles, temperatures recorded in a series running from the outside to the centre line rose to a maximum and then fell off. The red muscle was cooler than the white muscle at comparable distances from the body surface (Fig. 2). A sharper gradient was observed in another marlin, at the level of the lateral line opposite the middle pectoral fin, where temperature at a depth of 4 cm within the epaxial muscles was 0.45 degree C higher than at 2 cm, and 0.6 degree C higher than at 8 cm (the mid-line). Also in four other marlin, in three dolphin, two Sierra mackeral, one barracuda, and the black skipjack, at least one series of readings showed the temperature to be lower in the midline than within the lateral muscle mass. Carey and Teal (1966) observed the same phenomenon in tuna.

Temperatures within the viscera were always less than in the muscles. In five marlin the centre of the visceral mass was warmer than the sea surface (by from 0.65 to 1.25 degree C) but cooler than the maximum recorded muscle temperature (by from 0.75 to 1.50 degree C). In three dolphin and two Sierra mackerel mid-visceral temperature ranged from 0.5 degree C below to 0.8 degree C above that of the sea surface (the former probably due to the fish having come up from deeper cooler water) but the viscera were cooler than the warmest muscle by from 1.0 to 1.8 degree C in dolphin and from 0.35 to 0.5 degree C in Sierra mackerel. In one dolphin the mid-visceral temperature was 1.05 degree C cooler anteriorly where the visceral mass was wide (under the pectoral fins) than posteriorly where it was narrow (midway between the pectoral tip and the anus). Several other observations also suggested that temperature gradients within the visceral cavity were due to warming or cooling of the viscera from adjacent muscles or from the water.

Temperature in the pericardial cavity was the same as in the rectum, and 1.25 degree C lower than in the warmest muscles at that time, in a marlin 8 min after capture. A dolphin 8 min after capture also had a pericardial temperature below all muscle temperatures.

In all fish examined the antero-posterior location of highest internal temperature was opposite or just behind the pectoral fin. Dorsoventrally, highest internal temperatures were about 2 cm dorsal to the lateral line. In both planes, highest temperatures occurred in the vicinity of the thickest epaxial musculature.

Discussion.— In tuna subdued by curare, Carey and Teal (1966) observed higher temperatures in red than in white muscle. This difference might be anticipated, since it has been suggested that the well-vascularized red muscle metabolizes largely aerobically during steady sustained swimming, whereas the less vascular white muscle metabolizes anaerobically during bursts of activity (Bone, 1966; Stevens, 1968). Gordon (1968) showed that metabolic rates in unstimulated minced preparations of red tuna muscle were over six times as great as rates in white muscle, and Bilinski (1963) found in rainbow trout that fatty acid oxidation was more active in red than in white muscle. Probably heat production also is greater in unstimulated red muscle than in unstimulated white muscle. In subdued tuna, heat produced in white muscle would presumably be slight, and would be outweighed by heat produced in red muscle; the latter heat would be conserved by the countercurrent blood system enveloping the red muscle of tuna.

In contrast, in the present study on marlin the heat production in white muscle appeared greater than that in red muscle. However, the recordings on marlin were made under a completely different set of environmental and physiological conditions from those on tuna. Marlin were played on rod and line to exhaustion and then killed while in a presumably highly anaerobic condition. Under such a state of anoxia one might anticipate greater heat production in white muscle, a site of anaerobic respiration, than in red muscle. The present results probably approximate the thermal state in a marlin during

violent activity, as they were recorded shortly after the fish was landed. However, comparison with the natural situation is inexact. Heat loss from the muscle in a living fish would depend largely on removal of heat via circulating blood. In the present study the interference to the cardiovascular system from death is not known.

In the small sample of fish tested, species with a higher proportion of red muscle tended to attain higher body temperatures. Barracuda, which have temperatures only slightly above those of water, have relatively small lateral bands of red muscle. Dolphin and marlin attained quite high temperatures; the dolphin, although a smaller fish than the marlin, has well-developed red muscle not only in a superficial lateral band but also in diagonal streaks above and below each vertebra and, at least in the posterior portion of the body, in narrow bands along the vertebral column. In marlin the lateral red muscle band is quite well developed (Fig. 2) particularly towards the posterior. The black skipjack, which attained extremely high temperatures, has all its body muscles of a deep red colour (like fresh beef liver). Davy (1839) also reports high temperatures in several species of bonito and tuna which have "red or reddish muscle"; Carey and Teal (1966) cite records as high as 14 C above ambient.

Red muscle is probably not homologous in all fish. Moreover, differences in size and shape, and hence also in surface-to-volume ratios, may account for some of the observed temperature differences. (Sierra mackerel are relatively thin as well as relatively small.) Nevertheless, body temperature and extent of red musculature do seem roughly to be correlated. In a parallel fashion, Braekkan (1956) finds a general correlation between the extent and pigmentation of the red muscle and the speed and activity of fish within the series halibut, mackerel, herring, and bluefin tuna. Boddeke et al. (1959) find amongst freshwater species that "stayers" (capable of continued swimming) have a higher proportion of red muscle than do "sprinters."

The present data suggest that, although active species which produce much heat may have well-developed red muscle, the heat need not arise primarily in the red muscle, at least in the marlin under the conditions of this test.

The opportunity to make these observations aboard the M/V *Marijean* was provided by the interest and generosity of Dr H. R. MacMillan. The following enthusiastic assistants aided in the capture of specimens: Mr F. W. Bruce, Senator N. A. M. MacKenzie, Dr J. T. Sandy, Mr Ralph M. Shaw, and the Hon. James Sinclair. I have also been offered a great deal of constructive criticism by I. Barrett, E. G. Bligh, J. G. Eales, M. Freese, S. V. Manohar, D. J. Randall, and E. D. Stevens.

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Another Pink Salmon (*Oncorhynchus gorbuscha*) in its Third Year

In North America it has long been accepted that nearly all pink salmon mature in their 2nd year of life (Gilbert, 1914; Anas, 1959; Bilton and Ricker, 1965). In the USSR, for certain Asian stocks, Vedensky (1954) and Lapin (1963) have taken a different view. Vedensky considered that pink salmon usually mature in their 4th year, whereas Lapin concluded that a variable but sometimes fairly large proportion of each brood matures in the 3rd year and the balance matures in the 2nd year. These age interpretations have been contested (Bilton and Ricker, 1965). For North American pink salmon there has been to our knowledge only one individual reported as a 3-year-old (Anas, 1959): a female found in samples from the Skeena River, British Columbia, in 1956. The catch of a male in its 3rd year of life is reported here.

During the period November 21 to December 7, 1966, a total of 17 pink salmon was caught by salmon longlines at 6 stations of 11 fished in the Gulf of Alaska by the Canadian research vessel *G. B. Reed* (Turner and Barner, MS, 1967). These were frozen and taken to the Biological Station at Nanaimo, B.C. Subsequent examination of the scales of these salmon indicated that all except one had typical 1st year summer circuli and no annulus (Fig. 1). The scales of the exception, a male, one of seven pink salmon caught on December 7 at 51°30′N, 135°16′W, displayed the typical 1st-year summer circuli, followed by a band of compactly spaced circuli, the annulus, which in turn was followed by 23 second-summer circuli (Fig. 2). Presumably, if this fish had not been caught, it would have matured during its 3rd year of life or later. This specimen was identified as a pink salmon on the basis of external appearance and the identification was confirmed in the laboratory by comparing (Table I) the specimen's meristic counts with the ranges of counts given for Pacific salmon by Clemens and Wilby (1961) and by comparison of its scale characters with the scale structure key for identification of Pacific salmon (Bilton et al., 1964).

All the meristic counts for the specimen except the count of pyloric caeca fall within the range observed for pink salmon (Table I). The counts of gill rakers and lateral line scales suggest that this fish is a pink salmon.

The total number of circuli and the total scale radius in the atypical pink salmon (fish No. 3) were greater than those in the remaining six pink salmon in the catch (Table II) and were also greater than those in all other pink salmon caught during the cruise (for these 16 pink salmon the scale radius, measured from the centre of the scale focus along the longest anterior axis to the edge of the scale, ranged from 0.73 to 1.23 mm and averaged 0.99 mm. The number of circuli along the same axis ranged from 16 to 31 and averaged 24.43).

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TABLE I. Meristic counts for the atypical pink salmon, along with range of counts for pink salmon and possible species identification from the individual meristic characters (Clemens and Wilby, 1961).

	Count for atypical specimen	Range for pink salmon	Possible species identification from meristic count
Branchiostegals	11	9–15	So Co Ch Pi[a]
Rakers on first gill-arch	27	24–35	Pi Ck
Rays in dorsal fin	15	10–15	So Pi
Rays in anal fin	17	13–17	So Ch Pi Ck
Scales on lateral line	190	150–205	Pi
Pyloric caeca	158	165–195	Ck Ch

[a]So — Sockeye; Co — Coho; Ch — Chum; Ck — Chinook; Pi — Pink.

Comparison of the fork length and body weight of the atypical pink salmon with the lengths and weights of the six other pink salmon in the same catch supports the age interpretation (Table II). The fork length (50.0 cm) and weight (1270 g) of this pink salmon were well above the range of lengths (31.0–34.0 cm) and weights (250–360 g) of the six other pink salmon taken at the same time. The unusual size of this pink salmon at this time of year is even more apparent when it is compared with the size of pink salmon taken during exploratory winter fishing with longlines and gillnets conducted over a wide area of the Gulf of Alaska during the January–February periods of 1963, 1964, and 1965 (INPFC, Annual Reports for 1963, 1964, 1965). From a total of 57 pink salmon caught during these periods, fork lengths were recorded for 56 and body weights for 49. Fork lengths ranged from 26.0 to 39.5 cm, and body weights ranged from 140 to 450 g.

The gonadal development of the atypical male pink salmon (Table II) appeared to preclude any possibility of its being a very late 1966 spawner and indicated that it was an immature fish which would not have matured until 1967 or later. The weight of the gonads, expressed as a decimal fraction of the total body weight (maturity index of Godfrey, 1961), showed that the maturity index for the atypical pink salmon (0.031) was lower than any of the maturity indices for the six other pink salmon in the same catch. The fish also had a lower maturity index than all other males (nine) caught during the cruise; their indices ranged from 0.034 to 0.091.

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FIG. 1. Scale from a typical pink salmon caught December 7, 1966, showing first year summer circuli without an annulus.

FIG. 2. Scale from the atypical pink salmon caught December 7, 1966, showing first year summer circuli, an
lus (A), and second year summer circuli.

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TABLE II. Fork length, body weight, maturity index, and scale measurements of atypical pink salmon and each of six other pink salmon in the same catch.

Fish no.	Age	Sex	Fork length (*cm*)	Body weight (*g*)	Gonad weight (*g*)	Maturity index[a]	Scale radius 1st year (*mm*)	Scale radius 2nd year (*mm*)	Total scale radius (*mm*)	Number of circuli 1st year	Number of circuli 2nd year	Total circuli
1	0.0	M	33.0	320	0.2	0.063	0.98	–	0.98	28	–	28
2	0.0	M	32.5	270	0.1	0.037	1.23	–	1.23	26	–	26
3	*0.1*	*M*	*50.0*	*1270*	*0.4*	*0.031*	*0.90*	*1.06*	*1.96*	*26*	*23*	*49*
4	0.0	M	34.0	360	0.2	0.056	1.10	–	1.10	31	–	31
5	0.0	F	31.0	250	1.2	0.480	0.94	–	0.94	25	–	25
6	0.0	F	31.0	260	1.6	0.620	0.89	–	0.89	25	–	25
7	0.0	M	34.0	320	0.2	0.063	0.96	–	0.96	24	–	24
Avg[b]		M	33.4	317.5	0.17	0.055	1.06	–	1.06	27.2	–	27.2
		F	31.0	255.0	1.4	0.550	0.91	–	0.91	25.0	–	25.0

[a] $\frac{\text{Gonad weight}}{\text{Body weight}} \times 100$.

[b] Averages do not include data for fish no. 3.

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Diel Limnetic Occurrence of Young *Cottus asper* in Two British Columbia Lakes

The limnetic or planktonic occurrence of larvae and young-of-the-year cottids has been established recently for at least two species, *Cottus aleuticus* and *Cottus asper*. McLarney (1968) states that Bond (MS, 1963) was the first to have described the planktonic occurrence of larvae having cited Krejsa by personal communications to this effect. Laboratory experiments by Krejsa (1967) indicated the planktonic occurrence of *C. asper* larvae immediately after hatching. Heard (1965) described the appearance of planktonic *C. aleuticus* larvae in Brooks Lake, Alaska. Northcote and Hartman (1959) recorded a possible schooling behavior of young *C. asper* along a section of shoreline in Nicola Lake, British Columbia. These fish were recognized as yearlings rather than young-of-the-year, but nevertheless their schooling activity near the surface is noteworthy. Bond (MS, 1963), Hunter (1959), and Shapovalov and Taft (1954) documented the downstream migration of *C. asper* and *C. aleuticus*. Krejsa (1967) observed this same downstream migration followed by successful spawning and a planktonic larval stage in the estuary.

The following note describes observations of diel periodicity in the planktonic occurrence of young *Cottus asper* in two British Columbia lakes.

Methods.— Young sculpins were collected in 1964 at Buttle and Campbell lakes located on the Campbell River drainage system in the central portion of Vancouver Island, British Columbia. The sampling gear consisted of two rectangular nets (6 meshes per linear cm) attached one above the other in an aluminum frame of similar dimensions and design as used by Mundie (1959). This gear, which sampled a 0.5-m layer immediately beneath the lake surface, was towed at a steady slow speed (approximately 1.5 km per hr) for 10-min periods, straining about 105 m^3. Strong winds and rough water greatly restricted daylight towing in this program, primarily designed for sampling insect pupae and imagos at the lake surface. Therefore, all tows were made in the evening, usually beginning at 2100 hr and repeated at 2-hr intervals until 0900 hr PST. Location of stations and other sampling details are given in Sinclair (MS, 1965).

The very small fry could not be identified positively, but all larger and more-developed sculpins were *C. asper*. No other species of *Cottus* has been recorded from these lakes. Developmental stages in growth were recognized among the specimens, which were classified as stage 1 for those having incomplete fin ray development, whereas stage 2 fish had fully developed fin rays. All fish had completely resorbed yolk sacs.

Results and discussion.— The distribution of young cottids collected from three depth zones in each lake is given in Table I.

Length frequency distributions of the young cottids (not shown) suggest they represent a single age-class (0) in both lakes, although developmental

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TABLE I. Number of young cottids (stage 1 and 2) taken in surface tows (overnight) at Campbell and Buttle lakes.

Buttle Lake								
Depth (*m*)	Station	Stage	July 3	July 13	Aug. 10	Aug. 13	Aug. 24	Total
2	B6	1	2	0	2	1	1	6
		2	34	9	19	22	11	95
5	B5	1	1	0	1	0	1	3
		2	18	18	16	21	7	80
15	B8	1	2	1	0	1	0	4
		2	38	67	27	34	7	173
Campbell Lake								
Depth (*m*)	Station	Stage	July 9	July 27	Aug. 16	Aug. 19	Total	
2	L6	1	23	8	4	0	35	
		2	10	23	7	4	44	
9	L10	1	55	5	5	1	66	
		2	69	20	5	1	95	
19	L1	1	23	7	0	0	30	
		2	51	29	5	3	88	

stages were recognized (Table I). Of the young fish from Buttle Lake 96% were grouped in stage 2 with an average length of 10.5 mm (range 8–14 mm); the remaining 4% in stage 1, average 7 mm in total length (range 6–8 mm). In Campbell Lake, 64% were in stage 2 averaging 10.5 mm in length (range 8–12 mm); and the remaining 36% were classed as stage 1 with an average total length of 7 mm (range 7–9 mm). Although there was apparently no marked difference in spatial distribution between the two size-groups, there was an indication of seasonal change in their occurrence particularly in Campbell Lake. The maximum number of stage 1 fish in each lake and each station appeared in the first sampling day early in July, and then progressively decreased in abundance.

In Campbell Lake the peak of this limnetic occurrence was possibly very near the first sampling date, but perhaps a little earlier in Buttle Lake where the younger stage 1 fish were much fewer in number.

Although a complete 24-hr sampling series was not made, a definite diel periodicity was indicated for young cottids at the lake surface (Fig. 1). In Campbell Lake maximum catches were usually made between 2300 and 0500 hr during the night and relatively few or no young cottids were taken in early evening or morning samples. An obvious exception occurred on August 19 when minimum catches were made between 2300 and 0500 hr. There was dark overcast sky during the first sampling period that evening, but it became clearer and brighter by 2250 hr. From 2300 to 0215 hr the calm lake surface was brightly illuminated by a clear sky and full moon. At 0330 hr the light was considerably reduced when the moon disappeared behind the mountains.

In Buttle Lake a similar diel periodicity in surface occurrence of the young sculpins was indicated although larger catches seemed apparent during the 2100–2300-hr sampling period. In the last 2 sampling days in August

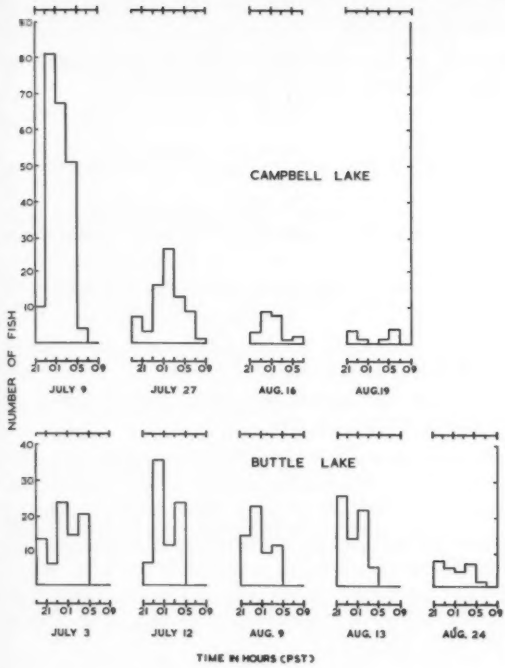

FIG. 1. Diel limnetic periodicity of young *Cottus asper*.

maximum catches first occurred at 2100 hr. Very few young cottids were taken between 0500 and 0900 hr in Buttle Lake, compared with catches in the same period from Campbell Lake (Fig. 1).

No definitive explanation for the nocturnal occurrence of young cottids near the lake surface can be offered at present. It may represent a means for dispersal or a period of feeding activity. Examination of stomach contents of 60 young from each lake revealed that 35% from Campbell Lake and 18% from Buttle Lake had recently been feeding. Northcote et al. (1964) suggested the diel vertical movement of peamouth chub may be a method of increasing the food source and feeding areas, and at the same time reducing the effectiveness of predators.

The marked diel periodicity in occurrence of young *C. asper* at the surface of lakes further adds to the complexity in the life history of freshwater sculpins, traditionally regarded as territorial bottom dwellers (Northcote and Hartman, 1959).

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Corrélation entre la structure rétinienne et l'habitat chez *Stizostedion vitreum vitreum* et *S. canadense*

Le doré jaune, *Stizostedion v. vitreum*, et le doré noir, *S. canadense*, sont des espèces sympatriques et montrent un phototropisme négatif marqué. Cependant, ils occupent des niches écologiques entièrement différentes. Le doré jaune se trouve généralement dans les eaux claires où sa croissance est maximale, mais il est aussi présent dans certains cours d'eau troubles. C'est un poisson plutôt crépusculaire, qui se nourrit surtout au point du jour et à la nuit tombante. D'autres part, le doré noir préfère les eaux troubles et se nourrit de façon plus active durant le jour. Il est également à noter que le jeune *S. v. vitreum* ne montre pas un phototropisme négatif aussi élevé que l'adulte (Ryder, communication personnelle).

Les yeux de ces deux espèces sont semblables dans leur morphologie externe. Moore (1944) a trouvé que la structure rétinienne du doré jaune peut être reliée à l'habitat de ce poisson, lorsqu'il la comparait à celle de *Hiodon tergisus*. Des corrélations semblables ont été établies par Wunder (1930) dans une étude approfondie sur quelques poissons du Lac Balaton en Hongrie. Dans la communication actuelle, nous présentons les résultats d'une étude histologique des rétines de ces deux espèces de doré. Les specimens du doré jaune provenaient des lacs Baptiste et Shebandowan, Ontario; ceux du doré noir, de la Baie Ombabika du lac Nipigon, Ontario, dont les eaux sont passablement troubles. La longueur totale de ces spécimens variait entre 421–538 mm (*S. v. vitreum*) et entre 269–379 mm (*S. canadense*). *Stizostedion canadense* croît plus lentement que *S. v. vitreum* et atteint des tailles plus modestes (Scott, 1967).

Les yeux, fixés dans la formaline (10%) ou dans le Bouin, furent enrobés à la paraffine, coupés à 6 μ d'épaisseur; puis les coupes étaient colorées à l'hématoxylène Harris d'abord, et à l'éosine ensuite. Différentes régions de l'oeil ont été examinées. La Fig. 1 montre des photomicrographies de coupes rétiniennes dans la région ventrale de l'oeil. La différence frappante entre les deux espèces se situe dans les proportions respectives de pigment mélanique et de guanine. Chez le doré jaune, le pigment épithélial rétinien est plus abondant que la guanine du tapetum rétinien, tandis que la situation contraire prévaut chez le doré noir. Rappelons que le premier préfère les eaux claires tandis que le second habite surtout les eaux troubles.

Il apparaît donc qu'une réduction du pigment épithélial et qu'une augmentation de la quantité de guanine permettraient au poisson de profiter au maximum de la faible intensité lumineuse de son milieu, en favorisant plus de réflexion de la lumière incidente à l'intérieur de son globe oculaire. Chez le doré jaune, d'autre part, il ne serait pas nécessaire d'augmenter la réflexion ni de réduire l'absorption, car la lumière disponible est plus élevée dans son milieu. D'ailleurs, tel qu'indiqué plus haut, le doré jaune semble

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préférer les périodes de la journée où la lumière disponible n'est pas maximale, et il est permis de soupçonner ce poisson d'utiliser quelquefois le peu de guanine rétinienne qu'il possède.

En ce qui concerne les autres aspects de la structure rétinienne tels que les cellules visuelles, les couches nucléaires, plexiformes et la ganglionnaire, nous n'avons pu noter aucune différence appréciable entre les deux espèces à partir du matériel à notre disposition. Il semble raisonnable d'assumer qu'il n'existe pas de différences majeures à cause de leur parenté taxonomique. De plus, ces éléments rétiniens d'origine nerveuse deviennent fixés au cours du développement de l'animal, et ne peuvent être modifiés qu'à longue échéance par des facteurs tels que les mutations. Par contre, les quantités respectives de mélanine et de guanine peuvent être modifiées plus ou moins rapidement en réponse aux exigences du milieu. Ces pigments sont des cristaux trouvés à l'intérieur des cellules épithéliales et sont des produits du métabolisme.

Il est étonnant que la structure rétinienne du doré jaune étudiée par Moore (1944) diffère de celle de la présente étude. Cet auteur observait une plus grande quantité de guanine et beaucoup moins de pigment mélanique que nous, description se rapprochant plus de celle du doré noir de l'étude actuelle. Moore (1944) précisait que la quantité de pigment épithélial était plus abondante à la périphérie rétinienne; nous avons aussi noté une légère variation, mais insuffisante pour expliquer le conflit entre ses résultats et les nôtres. Il est plus raisonnable de l'attribuer à des différences d'âge et/ou de milieu. Nous avons déjà indiqué que les jeunes dorés jaunes montrent un phototropisme négatif moins marqué. Ces deux espèces de *Stizostedion* ont probablement été pré-adaptées (dans le sens qu'utilise Walls, 1963) à vivre dans un milieu faiblement éclairé. Secondairement *S. v. vitreum* aurait évolué plus ou moins rapidement dans les eaux claires. Ceci expliquerait à la fois ce qu'obtient Moore et nous chez le doré jaune.

De plus, les cellules horizontales géantes décrites par Moore (1944) chez *S. v. vitreum* ne furent pas observées sur nos coupes. A certains endroits (Fig. 1), dans la couche nucléaire interne, ce qui nous apparaît comme des artefacts a possiblement été confondu pour des cellules horizontales par Moore. *Stizostedion canadense* ne présente ni ce type de cellules géantes, ni artefact de cette sorte.

Nous nous proposons d'entreprendre des études électrophysiologiques et spectrophotométriques afin de mieux comprendre les différences intra- et interspécifiques chez ces deux espèces du point de vue de l'âge et du milieu.

Nous désirons remercier le Dr R. A. Ryder, du Département des Terres et Forêts du Gouvernement de l'Ontario, pour avoir suggéré cette étude, ainsi que pour le matériel fourni. L'aide financière du Conseil National des Recherches fut également appréciée.

Summary. — Stizostedion v. vitreum *and* S. canadense *are sympatric species and both show a high degree of negative phototropism. However, they inhabit quite different ecological niches.* Stizostedion v. vitreum *generally inhabits clear water, where it attains good rates of growth. It is primarily*

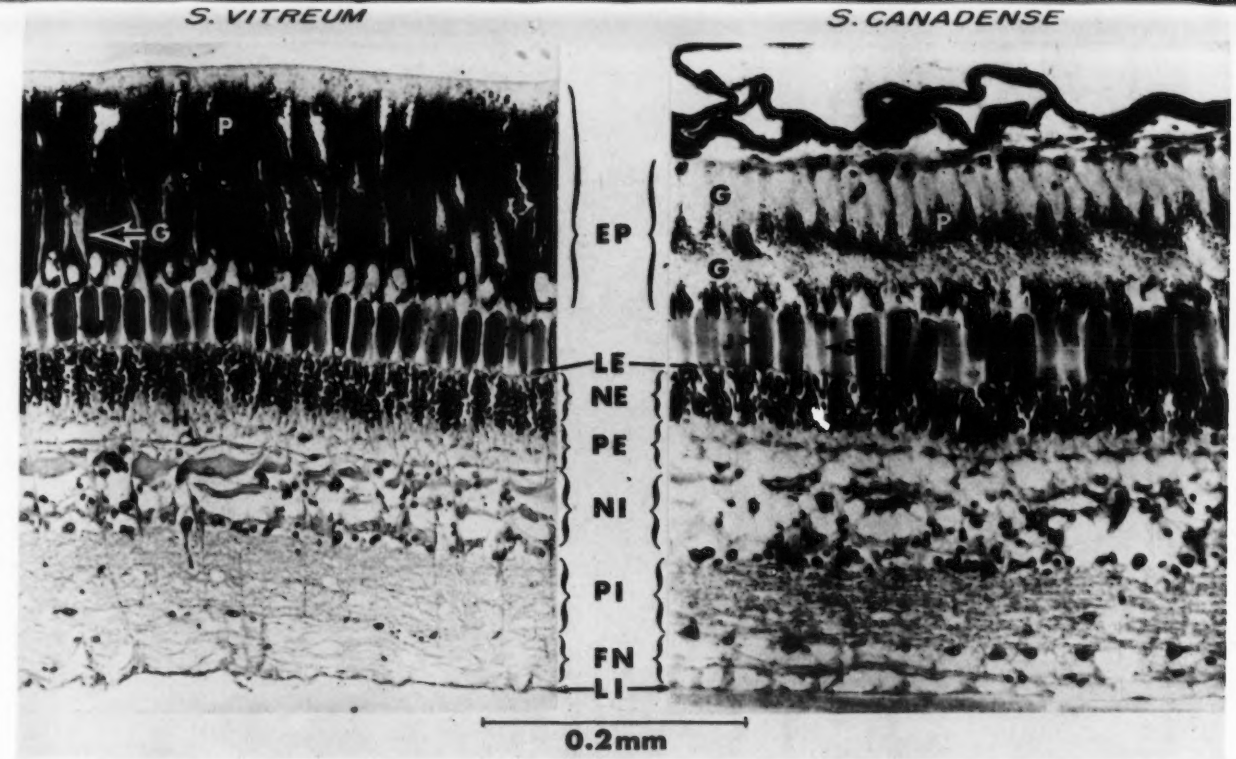

FIG. 1. Coupes transversales des rétines du doré jaune, *Stizostedion v. vitreum*, et du doré noir, *S. canadense*, dans la région ventrale. A noter la prédominance du pigment épithélial chez le premier et celle de la guanine chez le second. EP, épithélium pigmenté; FN, fibres nerveuses; G, guanine; H, cellules horizontales; J, cône jumeau; LE, membrane limitante externe; LI, membrane limitante interne; NE, couche nucléaire externe; NI, couche nucléaire interne; P, pigment mélanique; PE, couche plexiforme externe; PI, couche plexiforme interne; S, cône simple.

Cross-section of the retina of the yellow walleye, Stizostedion v. vitreum *and of the black walleye*, S. canadense, *in the ventral region. Note the predominance of the epithelial pigment of the first and the guanine of the second. EP, epithelium pigment; FN, nerve fibers; G, guanine; H, horizontal cells; J, double cone; LE, external limiting membrane; LI, internal limiting membrane, NE, external nuclear layer; NI, internal nuclear layer; P,* melanotic *pigment; PE, external plexiform layer; PI, internal plexiform layer; S, single cone.*

a crepuscular fish feeding at dawn and dusk. Stizostedion canadense, *on the other hand, grows well only in turbid water and despite a superficially similar eye feeds more actively throughout the day.*

The retinae of the two species resemble each other in structure except for the retinal epithelial pigment (REP). Stizostedion v. vitreum *has more REP and less guanine whereas the inverse is true for* S. canadense. *This variation is in good correlation with the differences in habitat and behaviour mentioned above.*

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Social Behavior among Juvenile Fall Chinook Salmon

Recent observations of extended freshwater residence of juvenile fall chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), by Reimers and Loeffel (1967) prompted this investigation of their social behavior as background to a comprehensive early life history study. Only a general outline of the social behavior of these fish in various environments is presented here.

The research was conducted in paired observation troughs and in the natural environment of Elk and Sixes rivers, short coastal streams near Port Orford, Oregon. The work was done during the spring and summer of 1965 and 1966. The lower parts of these rivers form two-layered estuaries, grading upstream into freshwater intertidal areas. The mouths of the rivers narrow just before entering the ocean, and at low tide are stream like, as nearly fresh water flows over the ocean beach. At high tide the mouths become inundated by full-strength sea water.

Numerous fall chinook salmon spawn in the tributaries of both rivers. Most juveniles move downstream out of the spawning tributaries from March through June as newly emerged fry. Some of the fish leaving the tributaries take up residence in the main river for several months, whereas others as small as 37–42 mm move directly into the estuary. Downstream movement from the tributaries does not occur after July, but in the main river movement continues and populations become small by late summer. By October two distinct populations usually exist: (1) many large fish (90–160 mm) in the estuary, and (2) a few small fish (50–90 mm) in the spawning tributaries. When the fall freshets begin, movement resumes and most fish leave the river and the estuary for the ocean, although some small fish remain and migrate as yearlings the following spring (Reimers, unpublished data, 1964–67).

Methods.— Social behavior was studied primarily in a pair of small observation troughs constructed alongside a tributary stream. Each trough was 2.40 × 0.60 m and consisted of two riffles about 0.13 m deep grading into an intermediate pool about 0.50 m deep. A flow of about 160 liters/min, containing drifting food organisms from the stream water source entered each trough from a head box. The riffle substrate was natural stream gravel supplied with additional intragravel water so that eggs and alevins could be planted in simulated redd conditions. Volitional residence was permitted in the observation troughs. Fish moving downstream passed out of the lower end of each trough and fell into a collecting trap. Each riffle and pool was viewed through a glass window from a darkened central observation area. The fish did not appear to be frightened by normal activities of the viewer.

Some experimental fish were seined from various areas and usually planted into each trough in groups of 50 fish. Others were obtained as eggs from adults captured on the spawning grounds and held in hatchery baskets until just before hatching or just before yolk absorption. About 250 were then buried

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20–25 cm under the gravel surface of the upper riffle of each trough and the fry allowed to emerge naturally. The fish were usually observed daily in experiments lasting from 7 to 60 days. Most observations were qualitative.

Observations in the natural environment in Elk River were confined primarily to Anvil Creek, a small tributary under intensive study. In Sixes River, observations were made in the tributaries, main river, and estuary. Most observations were made under water by snorkeling.

Agonistic behavior.— Juvenile fall chinook salmon exhibited agonistic behavior (Scott and Fredericson, 1951) in the observation troughs. In the experiments as a whole, the patterns of agonistic behavior, including nipping, lateral display, fighting, chasing, fleeing, submission, and redirected aggression, appeared to be similar to those described by Chapman (1962) for juvenile coho salmon, and resulted in territory formation in the riffles and hierarchy formation in the pools as described by Chapman (1962) and Hartman (1965) for juvenile coho. Fright huddle (Mason and Chapman, 1965) was also observed. In the natural stream environment all these behavior patterns except fighting, submission, and redirected aggression were observed.

Dominance–subordination relationships among the juveniles were largely determined on the basis of size as Chapman (1962) showed for juvenile coho salmon. Dominant chinook salmon possessed greater fin development and brighter coloration than subordinates, but the rapid color changes during social encounter described in other salmonids (Keenleyside and Yamamoto, 1962; Newman, 1956) were not noticed.

In most experiments lasting more than 2 weeks, one fish usually became clearly the dominant, defending the entire upper riffle during the experiment. This fish obtained more food and grew more rapidly than others. As an example, in one experiment 46 fish (average 40 mm; range 38–42 mm) were placed in the trough at the beginning of a 55-day experiment. All but four moved downstream. The emigrants were 43 mm or smaller and moved downstream early in the experiment. The dominant fish was 67 mm at the end of the experiment, whereas the other residents were 42, 46, and 49 mm. Similar results have been obtained for juvenile coho salmon (Mason, MS, 1966).

Aggregative or schooling behavior.— In addition to agonistic behavior in the natural stream environment of Sixes River, aggregative or schooling behavior (Breder, 1959) was observed several times in the large pools of the main river and commonly in the estuary.

Throughout the natural stream areas the distribution of juveniles was patchy. However, groupings of fish in particular areas rarely represented aggregations or schools. Close examination suggested that these groups were in locations where maintenance of position was possible and presumably food was abundant, such as eddy areas where fast riffles enter pools. These groups displayed agonistic behavior, which apparently led to the formation of size hierarchies.

In the estuary, where solitary fish were rarely observed, aggregations contained as many as several hundred fish. Individuals generally moved

freely within the group while feeding. When the fish were frightened they all oriented in the same direction and closed ranks. Several times large uniform schools were observed moving along the shore with smaller groups breaking away in an offshore direction. When schools moved inshore toward shallow water, they usually became disrupted and milling resulted. Schooling of juvenile fall chinook salmon has previously been reported in saltwater areas after release from Hood Canal Hatchery (Washington State Department of Fisheries, 1959).

Change from agonistic to aggregative behavior.— In the intertidal area of Sixes River, juvenile fall chinook salmon held stations, fed, and showed agonistic behavior during the ebb tide. As the tide flooded and the current slowed and eventually stopped, the fish rose off the bottom, aggregated, and foraged in many directions. When the tide again began to ebb, the fish again oriented into the current and agonistic behavior resumed. Whether the fish returned to the same stations is unknown.

Further evidence for the interchangeability of behavior was obtained in the mouth of Sixes River estuary during the ebb tide. Groups of 15–20 juveniles were observed in unstable depressions in the sand bottom created by the out-flowing current. These juveniles held positions, fed on drift, and showed some agonistic behavior even though they had presumably aggregated or schooled throughout the estuary before reaching this area. Where the outflow and ocean met, the fish oriented into the current. When an ocean wave came in the juveniles oriented toward the ocean, but when the wave receded they turned and faced the estuary. Observations at high tide were impossible in the river mouth because of turbulence.

Discussion.— The observations of juvenile fall chinook salmon exhibiting agonistic behavior in stream environments along with the residence data of Reimers and Loeffel (1967) suggest that some populations of this fish are well adapted for extended residence in fresh water. These observations raise the important question of whether behavioral mechanisms play a role in the numbers of juvenile fall chinook salmon that remain in fresh water in relation to the numbers that move downstream into the estuary. Territoriality and size hierarchies evidently led to adjustments in population sizes in the observation troughs, and regulation of density was probably in relation to food and living space (Chapman, 1966). But whether or not the large-scale downstream movement of fall chinook salmon fry that was observed in the natural environment resulted from agonistic behavior, as has been suggested for coho salmon fry by Chapman (1962), remains to be investigated.

Lister and Walker (1966) observed two periods of downstream migration of juvenile fall chinook salmon in the Big Qualicum River, a stream where total freshwater residence was completed by early summer. They hypothesized that density-dependent factors may be important in the movement of fry, since the output of late migrants was relatively small and constant compared with the large and variable fry migration.

Whatever factors led to differences in the length of freshwater residence and the associated dispersion of fish of nearly the same age from the headwaters

to the estuary, the juveniles appeared to be opportunistic in their behavior. Juveniles that moved downstream exhibited aggregative or schooling behavior, survived, and grew rapidly, as the field sampling showed.

Additional studies are needed to elucidate the ecological significance of the different types of behavior and the role of behavioral mechanisms in the dispersal of juvenile fall chinook salmon throughout the environment.

I appreciate the aid of biologists of the Fish Commission of Oregon in conducting this work. Drs J. D. Hall, Oregon State University, G. F. Hartman and N. R. Liley, University of British Columbia, D. W. Chapman, University of Idaho, Mr R. E. Loeffel and Dr J. M. Van Hyning, Fish Commission of Oregon, offered encouragement and valuable comments.

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